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JOURNAL
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VOL. 49 DECEMBER 1959 No. 10

ASTRONOMY.—Cepheid variables and the period-luminosity relation.[1] C. PAYNE-GAPOSCHKIN, Harvard College Observatory. (Communicated by Charles M. Herzfeld.)

The period-luminosity relation has almost reached its fiftieth anniversary. Today it is being studied more actively than ever, and its observed complexities and theoretical implications are still far from exhausted. In fact I hope to show that what we know and understand at present about the period-luminosity relation is far less than what remains to be discovered and interpreted.

Introduction.—The diagram derived by Miss Leavitt (*1*)[2] from 25 Magellanic Cepheids, reproduced in Fig. 1, already shows several of the features of current interest: the linear relationship between the apparent magnitude and the logarithm of the period, the scatter of the points about the curve, and the variety of amplitudes. Each, as I shall describe, has been verified and amplified by later work.

The earlier work of Bailey (*2*) on the variable stars in globular clusters laid the foundation for the recognition of an equally striking relationship between period and apparent brightness within any one globular cluster. Although the variables with periods shorter than a day showed no marked correlation between period and brightness, the few with longer periods were always brighter. On the simple assumption that all the short-period variables were of similar luminosity, Shapley (*3*) constructed a period-luminosity curve from the data for all globular clusters that contained variables with periods longer than a day, and concluded that it had the same slope as the relation for the Magellanic Cepheids.

If the identity of the two period-luminosity relationships is granted, the conversion from apparent to absolute magnitude can be effected by the establishment of absolute magnitude for some one contributor to the curve. The short-period variables in globular clusters were identified with the RR Lyrae stars of the galactic field, many of which have periods and light curves exactly like those of the cluster variables. Accordingly the absolute magnitudes of the RR Lyrae stars were intensively studied, and the generally accepted value 0.0 was used to fix the zero point of the period-absolute magnitude relation.

The immediate application of this conclusion by Shapley led to his epoch-making study of the dimensions of the galaxy. Later revisions of this work have resulted from improvements in the scale of apparent magnitudes and from corrections for obscuration, not from revisions in the zero point of the absolute magnitudes.

The upper part of the period-luminosity curve was used to derive the distances of the Magellanic Clouds, and when Hubble (*4*) discovered Cepheids in NGC 6822, Messier 33, and Messier 31, the distances of these galaxies were similarly derived. These applications of the period-luminosity curve depended on the original working assumption that the relationships among the stars in globular clusters and those in the Magellanic Clouds and other galaxies were not only parallel but identical. That this assumption is not justified was shown by Baade (*5*) in his study of the Andromeda galaxy. The zero point of the period-lumi-

[1] The 28th Joseph Henry Lecture of the Philosophical Society of Washington, delivered before the Society on May 22, 1959.

[2] Italic numbers in parentheses refer to the Bibliography, pp. 349–350.

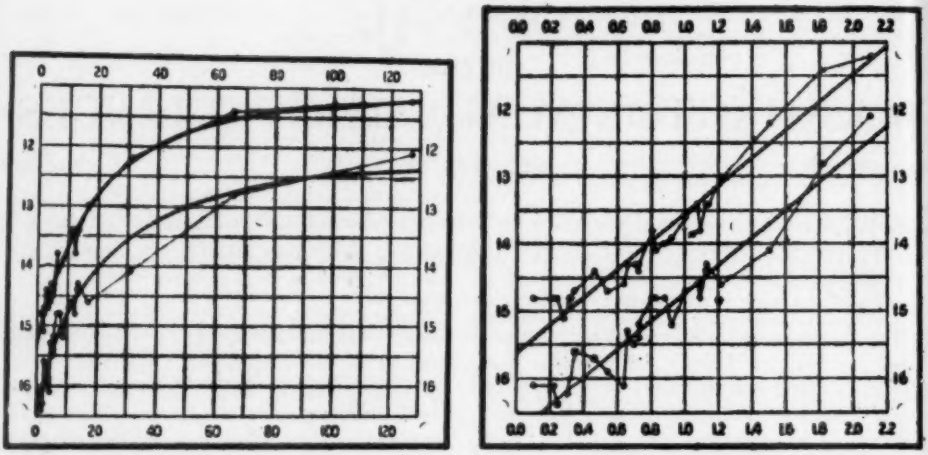

FIG. 1.—Miss Leavitt's period-luminosity relation (maximum photographic magnitude above, minimum below). Left: period plotted against magnitude; right, logarithm of period plotted against magnitude. From Harvard Circular 173. 1912.

nosity curve for classical Cepheids was thus revised upward by about 1.5 magnitudes, and all distances derived by the use of the upper part of the curve were accordingly also revised upward.

Within any one globular cluster there is very little correlation between the apparent magnitude and period of the RR Lyrae stars, but the photographic (though not the photovisual) magnitude has been shown for example by Roberts and Sandage (*6*) to be slightly brighter for the variables of shortest period in Messier 3. That the absolute magnitudes of RR Lyrae stars may differ slightly in different globular clusters is suggested by Sandage (*7*) and the possibility that the accepted absolute magnitude of RR Lyrae stars may require downward revision is discussed by Arp (*8*).

The period-luminosity relations for variables in globular clusters and for Cepheid variables have been convincing separated by the work that has been briefly sketched in the preceding paragraphs. Another equally striking correlation that might well have pointed in the same direction many years ago is the Hertzsprung relationship between the periods and the forms of the light curves (*9*). The classical Cepheids of the galaxy show a progression in the form of a light curve (*10*), such that stars of the shortest periods show a smooth rise and fall, at longer periods (about 5 days) a hump appears on the declining side, and becomes more pronounced up to periods between 8 and 9 days. Between 9 and 10 days the curves abruptly become more symmetrical, with a more or less well-marked hump between two shoulders, and generally small amplitude. At rather longer periods the light curve has a more abrupt and asymmetrical rise, with a small hump just preceding the main brightening, and at the longest periods the curve is again found to be smooth and uncomplicated. The light curve thus runs through one complete cycle of changes between the shortest and longest periods. Cepheids in the Magellanic Clouds also display the Hertzsprung relationship (*11*).

An analogous relationship between period and light curve is shown by the short-period variable stars in globular clusters: in any one cluster, the stars of shortest period have light curves that are almost sine curves, and there is a rather abrupt transition at some longer period (not the same in all clusters) to a highly asymmetrical light curve, usually with a small hump before the main rise. Stars of the longest periods (less than a day) have less asymmetrical light curves. This relationship was

pointed out by Bailey, who designated the curves by the letters c, a, b, in order of increasing period.

The Hertzsprung relationship for galactic classical Cepheids and RR Lyrae stars is illustrated in Fig. 2.

The globular cluster stars with periods over a day do not conform to the Hertzsprung relationship; those with periods between 10 and 20 days show a broad maximum or a hump on the downward slope (*12*). A few galactic variable stars of simi-

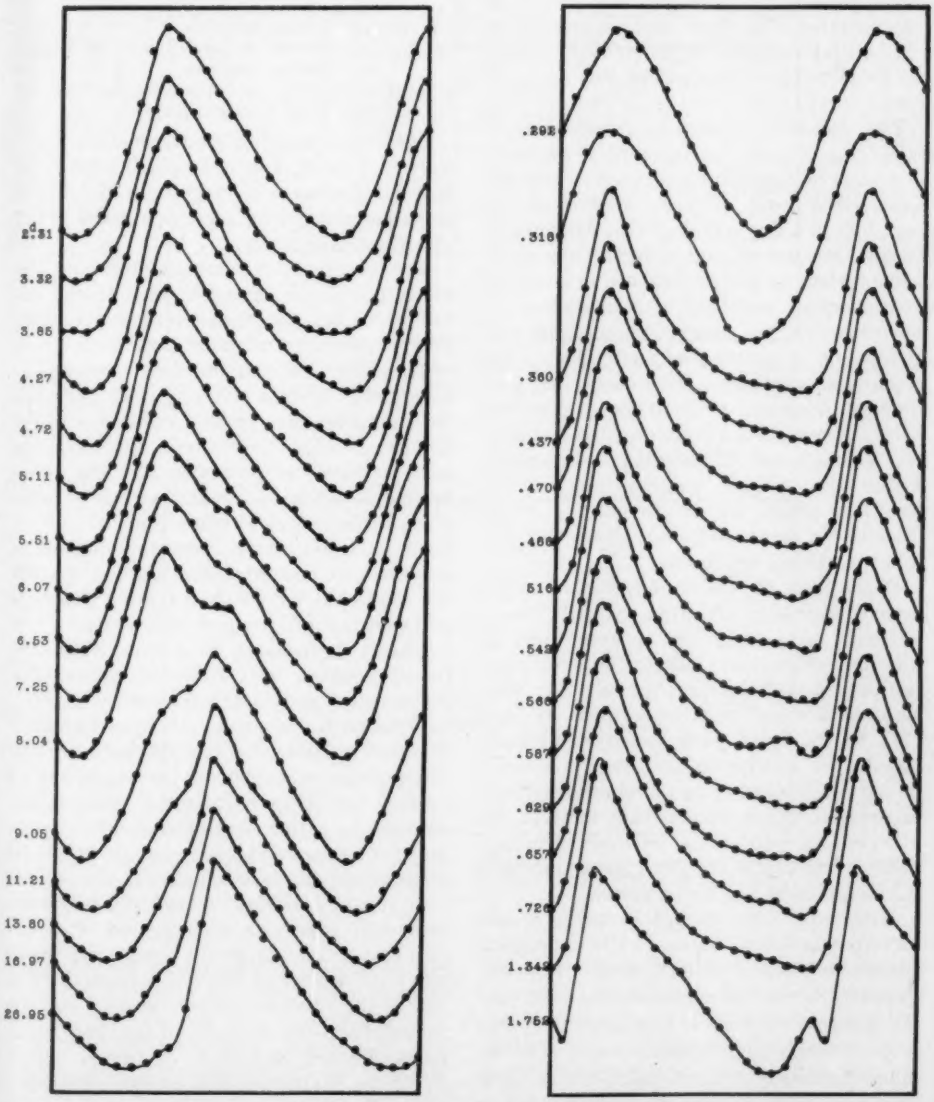

FIG. 2.—The Hertzsprung relationship: means for Classical Cepheids (left); means for galactic RR Lyrae stars (right). From Harvard Annals, 113. 1954.

lar period, which differ from classical Cepheids in lying far from the galactic plane, in motion, and in other ways, show similar light curves. In particular, a group of Cepheids associated with the galactic center shows a period-light curve pattern similar to that of the stars in globular clusters (*13*). These galactic variable stars are clearly to be associated, like those in globular clusters (*14*), with Population II, whereas the classical Cepheids are members of Population I (*15*).

The period - luminosity relationship.— Miss Leavitt's period-luminosity relationship showed considerable scatter about the mean curve, and all later studies of the variables in a single system (the Magellanic Clouds, Messier 31, and so forth) also show a dispersion. As the periods are determined with adequate accuracy, it is usual to consider whether the observed dispersion can be a result of factors that have affected the magnitudes. Shapley (*16*) enumerated possible contributors: errors of the magnitudes, effects of unresolved doubles, effects of general background brightening, obscuration within the system, galactic obscuration, Eberhard effect. Erroneous periods would produce the same effect, but their contribution is certainly negligible.

In the early days of the application of the period-luminosity relation, there was a tendency to assume that a great part of the dispersion was due to observational causes and that the stars actually lay very close to the curve. Recent work by Arp (*17*) on the Small Magellanic Cloud leads him to the conclusion that most Cepheids lie within a range of one magnitude at any one period, which implies that most of the observed dispersion is intrinsic. Sandage (*18*) contemplates the even larger range of 1.2 magnitudes at a given period.

Hitherto I have spoken in terms of observed quantities only. Further progress cannot be made without some very elementary theoretical assumptions: first, that the relationship $P\sqrt{\rho} = C$ is accurately fulfilled; second, that Cepheids conform to the mass-luminosity relationship. Granted these premises, then if there is a dispersion in magnitude at a given period, three conclusions follow:

1. At a given period there is:
   (a) a dispersion in color, the bluest stars being of highest luminosity
   (b) a dispersion in luminosity, the brightest stars being the bluest
2. At a given luminosity, there is:
   (a) a dispersion in period, stars of longest period being the reddest
   (b) a dispersion in color, the reddest stars being of longest period
3. At a given color, there is:
   (a) a dispersion in period, stars of longest period being brightest
   (b) a dispersion in luminosity, the brightest stars being of longest period

These three conclusions are shown graphically in Figs. 3, 4, and 5, which have been drawn for a range of magnitude of 1.0 at a given period, and for a range of color of 0.2 at a given magnitude.

The relation between mean color and absolute magnitude is not implicit in the assumptions, but can be shown to be plausible. The existence of a mean period-spectrum relation for Cepheids has long been recognized, and the data given by Code (*19*) define it accurately. If all Cepheids were of the same color, they would all have the same surface temperature. But the more luminous Cepheids would then have somewhat earlier spectral classes on account of lower surface gravity. Since the opposite is observed, we can infer that bright Cepheids are somewhat redder than fainter Cepheids and that the difference of color between two Cepheids is greater than the difference found between two stars of comparable luminosities and identical spectral class.

Data on the accurate colors of Cepheids in other galaxies are needed, both to test the qualitative statements just made and to provide quantitative material from which consistent period-magnitude-color arrays may be constructed. However, the effect of obscuration also enters into such colors, and even if all Cepheids in a system were of the same true color at a given period, obscuration and extinction would conspire to make the most reddened stars the faintest. The size of the effect in our own system may be judged from the diagram of maximal color index against logarithm of period reproduced by Walraven, Muller and Oosterhoff (*20*). The diagram contains a few points for the two Magellanic Clouds, from measures by Gascoigne; these, and the few colors

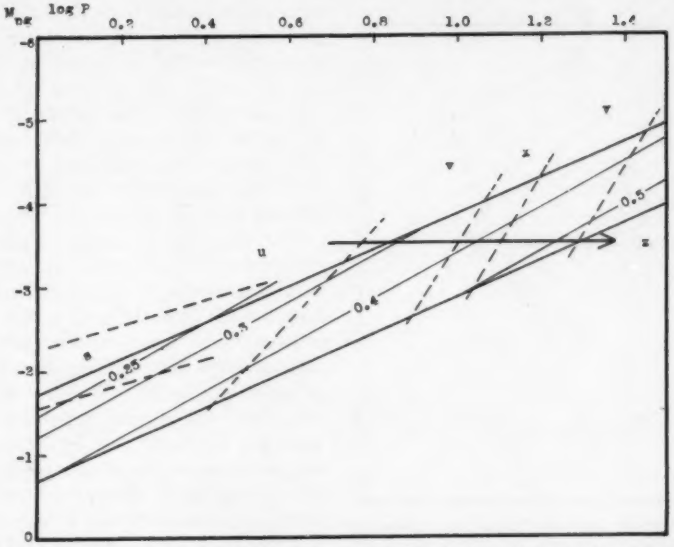

FIG. 3.—Relation between period and absolute magnitude (schematic); light lines show equal colors; broken lines separate the domains of different curve types. The arrow shows the possible course of Cepheid development.

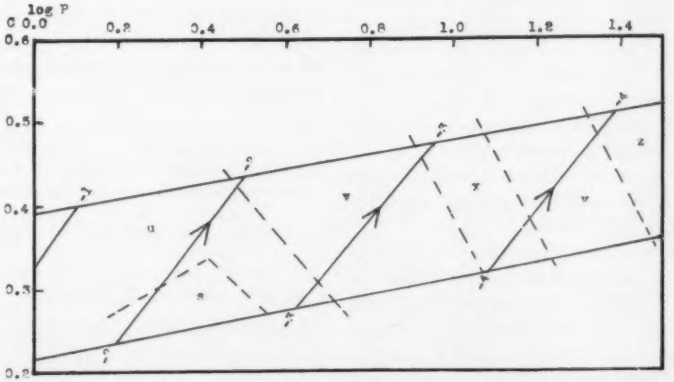

FIG. 4.—Relation between period and color (schematic). Light lines show equal absolute magnitudes; broken lines separate the domains of the different curve types. Arrows show the possible course of Cepheid development.

published or discussed by Gascoigne and Kron (*21*), Gascoigne (*22*), and Gascoigne and Eggen (*23*) are not inconsistent with the view here expressed. Gascoigne and Eggen act on the belief that the evidence for identity in color between galactic and Magellanic Cepheids, though not conclusive, is encouraging. Opinion has long been divided on this matter, and I will state my own view—that the colors of the galactic and the Magellanic Cepheids are essentially similar, and that the dispersion of color is as decribed above in simplified terms.

The Hertzsprung relationship.—The relation between the period, luminosity, and light curve of a Cepheid must next be con-

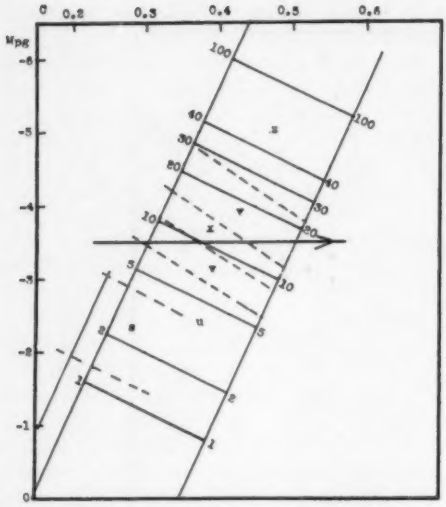

FIG. 5.—Relation between color and absolute magnitude (schematic). Light lines show equal periods; broken lines separate the domains of the different curve types. The arrow shows the possible course of Cepheid development.

sidered. The fact that averaged light curves for several stars with a small range of period display the Hertzsprung relation shows clearly that form of light curve is closely related to period. If the period-luminosity curve has a dispersion, then, if stars of a given period should have identical light curves, stars of a given absolute magnitude should have light curves that differ systematically with period.

The Cepheids in the Small Magellanic Cloud furnish information on this point. In order to present the data something must be said about the classification of light curves. The Bailey types a and c for the variables in globular clusters are excellent criteria, unambiguous and mutually exclusive. Type b, however, grades into type a and today is usually combined with it. In the classification of light curves, as in other matters (period frequencies, absolute luminosities of RR Lyrae stars) a globular cluster appears, so to speak, to lack a dimension in comparison to a system like the Small Cloud. This dimension is very likely mass: stars on the horizontal branch of a globular cluster must all be of almost the same mass. The Cepheids in a large system also differ in the time dimension. Methods of analysis and classification that give clear-cut results for globular clusters will not necessarily do so when applied to more complex groups. This statement, obvious in regard to color-magnitude arrays, is no less true of the classification of light curves. Methods that suffice for RR Lyrae stars are not flexible enough for Cepheids.

The first photoelectric light curves of Cepheids confirmed the variety and complexity of the light curves and color changes. Eggen (*24*) first defined groups A, B, C to represent the light curves, on the basis of relationships between period and amplitudes of light and color. Whether or not is was intended, the names suggested a parallel with the Bailey types, which has no physical justification. In a later paper, the definitions for types A, B, and C have been modified: a star is of type C if the light curve is symmetrical ($M - m = 0.37\,P$), of type B if a hump is present, of type A if no hump is observed (*25*).

To me it has always seemed that the Hertzsprung relationship is fundamental in describing the light curves of Cepheids, and that three classes are not enough to cover its complexities. My own classes have been defined as follows (*26*)

u: smooth, asymmetrical (δ Cephei)
v: smooth rise, hump on decline (η Aquilae)
w: saddle-shaped curve (S X Velorum)
x: central peak, shoulder on each side (Z Lacertae)
y: sharp rise, preceded by small rise (S Z Aquilae)
z: smooth, asymmetrical (U Carinae)
s: sine curve (G H Carinae)

Eggen's type C covers types s and x, his B covers v and w, and his A covers u, y, and z.

The period-luminosity curve for minimal photographic brightness in the Small Magellanic Cloud is shown in Fig. 6, which embodies a great deal of unpublished material kindly made available by Dr. Shapley, for over 600 stars. The magnitudes are on the uncorrected Harvard scale; Arp's photoelectric work has shown that the range of magnitudes should be increased.

The points corresponding to stars with different curve types have been plotted with distinctive symbols, and I have indicated by

FIG. 6.—Relation between logarithm of period and apparent minimal magnitude for Cepheid variables in the Small Magellanic Cloud. Stars with various types of light curve are shown as follows: type s, circles; type u, dots; type u-v, half-filled dots, vertically divided; type v, crosses; type w, circled crosses; type x, circled dots; type y, circles horizontally divided; type z, dots (= type u). Light lines separate the domains of the various curve types.

broken lines the approximate domains occupied by light curves of different types.

An earlier diagram of the same kind (*26*) made with about a hundred stars from both clouds shows the effect more clearly. This is in part because the light curves were better determined, in part because the stars were selected for freedom from obvious obscuration. The reality of the dependence of curve type on luminosity as well as on period was verified by means of the χ^2 test. Points for curve type u could not be included in the discussion on account of incompleteness at faint magnitudes.

A feature of Fig. 6 that does not run parallel to the other curve types is the group of symmetrical curves for stars of short period. These small-range curves seem to follow a period-luminosity spread parallel to the main one, and overlapping it slightly. These stars are of such interest that they must be examined critically to see whether their small range, and comparatively high luminosity for their period, could result from the presence of unresolved companions. They seem to be too numerous for this to be a likely interpretation. Moreover, they have counterparts in our galaxy (GH Carinae, FF Aquilae, DT Cygni).

Cepheids of similar curve type, therefore, are not aligned precisely with Cepheids of similar period. In Figs. 3, 4, and 5, the domains of similar curve type are separated by broken lines. These domains cut lines of equal period (mean density), equal luminosity, and equal color, at various angles, so curve type is not primarily determined by any of these properties of the star.

Development of RR Lyrae stars.—The place of the RR Lyrae stars in stellar development has been deduced from their well-defined position in the H-R diagrams of globular clusters. They are evidently members of the horizontal branch; the continuity of star counts through the variable star domain, in variable-rich clusters, suggest that they move *along* the horizontal branch (*27*). The correlation of period and color found in Messier 3 by Roberts and Sandage implies that an RR Lyrae star changes its period as it crosses the gap, and makes an abrupt transition to or from "overtone" pulsation as it crosses the interface between the type a and c curves. Changes of period are not (and are unlikely to be) large enough to indicate which way the RR Lyrae star travels in the H-R plane although one can infer that many writers think in terms of progress from long to short period, from fundamental to overtone, from right to left in the HR plane.

If the method of mapping empirical evolutionary tracks employed by Sandage (*28*) is valid, the distribution of stars along the horizontal branch might give a clue to the rate at which a star crosses the variable gap, or at least the relative rate at which different parts of the path are traversed. As Arp (*29*) has pointed out, a strongly populated horizontal branch goes with a large variable star population, but there are variable-poor clusters such as Messier 2 in which only one side of the variable star gap is well populated. Within the gap itself, however, the variable stars are not distributed uniformly with period. In ω Centauri, for example, numbers of stars within equal limits of log P are as follows:

log P	0.4 to 0.5	0.5 to 0.6	0.6 to 0.7	0.7 to 0.8	0.8 to 0.9	0.9 to 1.0
Number of stars	6	31	15	38	25	10

These numbers do not change uniformly, as might be expected for steady progress across the gap; rather they suggest acceleration-deceleration-acceleration as the gap is crossed. For classical Cepheids the situation is even more complex. In any one globular cluster there is a very small dispersion of absolute magnitude at any one period, but in a large stellar system such as the Magellanic Clouds and Messier 31, the dispersion in magnitude at one period adds at least one dimension to the problem.

Development of Cepheids.—It has long been recognized that the Cepheid variables lie within the Hertzsprung gap in the HR plane. Although the true colors of galactic Cepheids, and their dispersion, are extremely difficult to determine, as has already been mentioned, it seems very likely that all Cepheids with a given luminosity lie within a restricted range of color (about 0.2 magnitude), and that no other stars lie within this range. The Population II Cepheids seem to occupy a similar domain,

probably somewhat to the blue of the domain for classical Cepheids. The situation as I see it is shown in Fig. 7. The variable supergiants appear to lie on either side of the Cepheid domain (*30*).

The picture has been refined by the discovery of a few Cepheid variables in galactic clusters (*31*). The well-established members are tabulated below.

Cluster	Cepheid	Period d	Light curve	
			Eggen	This paper
NGC 6664	EV Sct	3.09	C	s
NGC 7788	CE Cas a (*32*)	4.45		
	CF Cas	4.87	AB	u
	CE Cas b	5.13		
Messier 25	U Sgr	6.74	AB	v
NGC 129	DL Cas	8.00	C?	a?
NGC 6087	S Nor	9.75	C	x

The suggestion of Bidelman that UX Persei ($4^d.57$), UY Persei ($5^d.37$), VX Persei ($10^d.90$) and SZ Cassiopeiae ($13^d.60$) are members of the Perseus I association should be mentioned (*33*). The Burbidges regard SZ Cassiopeiae as "probably a member of the cluster." The apparent magnitudes of all four stars are correlated with their periods.

The stars in the table are all as bright as, or brighter than, the brightest main sequence stars in the clusters (*34*); the four possible members of the Perseus cluster are fainter than the bright B stars and M stars in the Perseus double cluster. These data suggest that the age of a Cepheid in a galactic cluster can be determined:

Star	Cluster	Age of cluster years	Age of Association years	*Ref.*
EV Sct	NGC 6664	2×10^8		(*33*)
CE Cas a CF Cas CE Cas b	NGC 7788	10^8		(*33*)
U Sgr DL Cas S Nor	Messier 25 NGC 129 NGC 6087			
SZ Cas	h, χ Persei	10^8		(*35*)
	Perseus I		4×10^8	(*36*)

The Cepheids in galactic clusters evidently lie within the Hertzsprung gap, and it is rather clearly indicated that a star becomes a Cepheid as it reaches a certain critical color as it crosses the gap. Analogy with globular clusters, where nonvariable stars are found on both side of the gap, might suggest that it emerges on the other side of the gap and becomes a red giant, and at least in NGC 6664 there is clear evidence of red giants (*31*). If SZ Cassiopeiae is a member of the Perseus Association, it again is associated wtih red giants, and ER Carinae has been suggested as a possible (though unverified) member of NGC 3532, which is very rich in red giants. We note also that the lower limit of the classical Cepheids is not far from the place (between NGC 752 and Messier 67) where the Hertzsprung gap has narrowed and disappeared. The general picture is shown in Fig. 8, which amplifies Sandage's well-known diagram by the addition of material for the Orion I association (*37*) and the Magellanic Clouds (*38*).

The three Cepheids in NGC 7778 display a rather small range of periods and magnitudes. The bright "galactic" cluster NGC 1866 in the Large Magellanic Cloud is an example of a cluster that contains many Cepheids, most of them in a restricted range of period (*39*). The following table gives the names, periods, and approximate mean magnitudes; stars within 10′ of the center of the cluster are marked with asterisks.

HV	Period d	Mean m_{pg}	HV	Period d	Mean m_{pg}
12206*	2.506	16.1	12194*	3.205	16.0
12208	2.604	16.2	12205*	3.210	15.9
12199*	2.639	16.51	12189	3.246	16.4
12200*	2.725	16.4	12187	3.287	15.8
12209	2.930	16.21	12204*	3.439	15.6
12188	2.934	16.31	12201*	3.444	15.8
12211	2.940	16.21	12193	3.465	16.3
12203*	2.954	16.4	12198*	3.523	16.2
12202*	3.101	16.2	12207	4.566	15.8
12196*	3.113	16.4	12211	5.083	15.9
12197*	3.144	16.01	12186	12.24	15.0
12195	3.190				

Most of the Cepheids in NGC 1866 lie within the limits 0.40 and 0.55 in log P, and there is a trend toward brighter magnitudes for longer periods. The picture is like that presented by nearby galactic clusters, except that NGC 1866 is much richer in

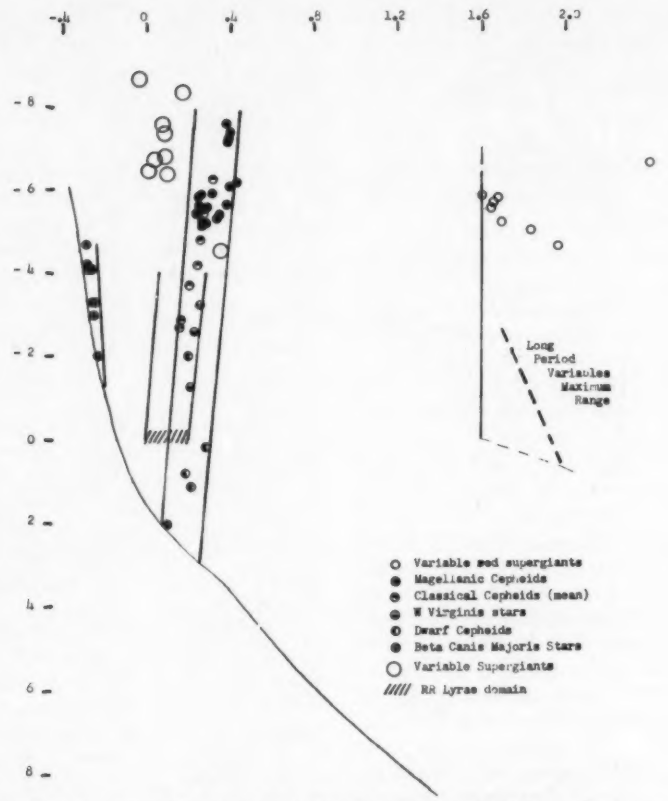

FIG. 7.—Domains of the several types of variable stars in the color-magnitude array. The original main sequence is sketched as a light line.

Cepheids. Details of its color-magnitude array will be of extreme interest. If there is a detailed analogy with galactic clusters, we can infer an age comparable with that of EV Scuti from the average period of the Cepheids. With the anticipated discovery of more Cepheids in Magellanic clusters, we can look forward to verification and extension of the dating procedure.

Galactic clusters provide suggestive qualitative information about the course of development of a Cepheid; among other things they suggest that the Cepheids follow a route like that of stars of mass over 2.5 suns, and move more or less horizontally across the HR plane, rather than rising sharply after leaving the main sequence, like stars of solar mass and less. This is the justification for the earlier assumption that Cepheids conform to the mass-luminosity relation.

In a globular cluster, there is a strong correlation between the amplitudes and periods of the RR Lyrae stars, which we have mentioned as probably traversing the horizontal branch across the variable gap: as we go from long to shorter period, the amplitude rises to a maximum, and then falls abruptly at the transition between curves of type a and type c. In NGC 1866 we note that four stars of amplitude 1.2 magnitudes and more lie between log $P = 0.5$ and 0.54, but there are also two stars of large amplitude with log $P = 0.41$, one of them within 10′ of the center of the cluster. The numbers of stars within equal limits of log P are:

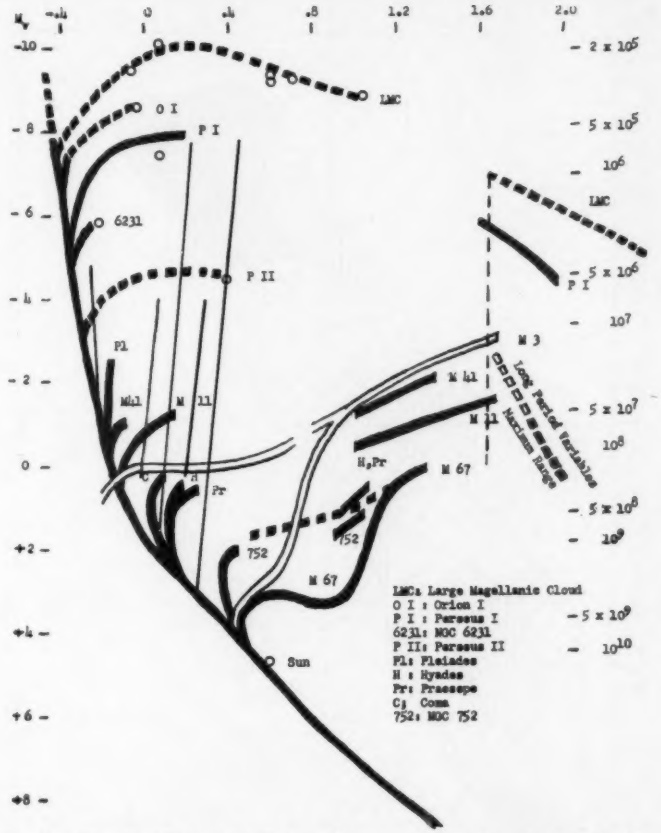

FIG. 8.—The Cepheid variable domain as related to the color-luminosity arrays of galactic clusters and associations.

log P	0.4 to 0.45	0.45 to 0.5	0.5 to 0.55	0.65 to 0.7	0.7 to 0.75	over 1.0
Number of stars	4	7	9	1	1	1

Thus the greatest concentration of periods coincides with a maximum of amplitude. Here again there is no indication of steady progress through the gap, but of a slowing-up in the neighborhood of log $P = 0.525$.

A single cluster presents a simpler picture than the Cepheids in a larger system; its stars may be regarded as having dispersion in mass, but do not differ appreciably in age. It is not surprising that the Small Cloud displays no simple relation between period, luminosity and mean amplitude. Fig. 9 shows a contour map of mean amplitudes in the period-luminosity plane. Small amplitudes are characteristic of periods between 8 and 10 days and apparent magnitude 15.4 (about absolute magnitude −3.6), and also of the strip to the short-period edge of the diagram for apparent magnitudes less than 16.0. These latter small amplitudes correspond to the type s light curves of Fig. 6. The fact that they are associated with the shorter periods speaks against the possibility that they are caused by unresolved companions, for there is no reason why unresolved companions should have a preference for particular *periods*; they should be equally common at all periods for a given apparent magnitude. Large amplitudes show an even more striking distribution. They occur, as is well

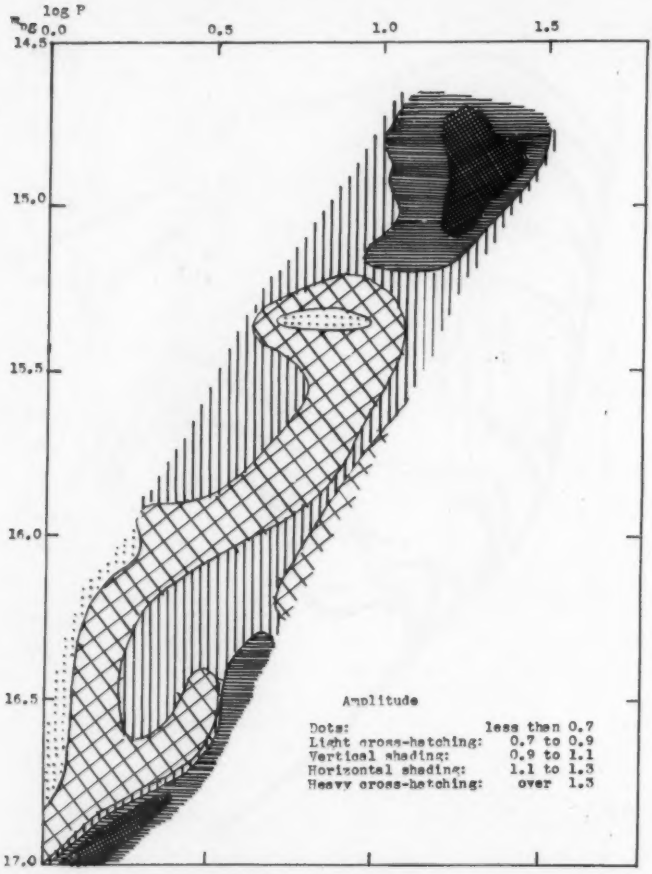

FIG. 9.—Mean amplitudes of the Cepheids in the Small Magellanic Cloud (schematic contour diagram).

known, for the more luminous stars, but they also occur at the low-luminosity, long-period edge of the period-luminosity array. The occurrence of large amplitudes among the fainter Magellanic Cepheids has been noted by Arp and is undoubtedly a real phenomenon.

If the path of any one Cepheid is a horizontal track across the period-luminosity plane, we might be able to trace the changes that a star undergoes by examining the changes in light curve at any one apparent (and therefore absolute) magnitude with changing period. Figs. 10, 11, and 12 show such series of light curves at seven different apparent magnitudes, and are typical for the whole available material. At brighter magnitudes, the light curve shows systematic changes and shifts of one prevalent pattern, which recall the Hertzsprung relationship, and illustrate the angle at which light curves of different types cross the average period-luminosity relation. For fainter magnitudes, however, the stars of shortest period tend to have small-amplitude, symmetrical light curves (type s), which recall the type c light curves for RR Lyrae stars in globular clusters.

If it is accepted that a Cepheid travels from left to right in the HR plane, and if

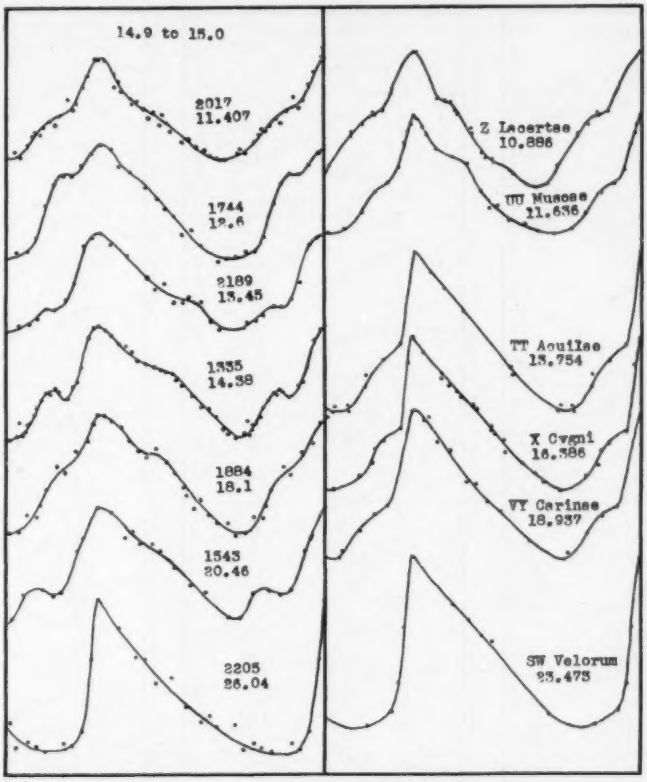

FIG. 10.—Light curves of Cepheids in the Small Magellanic Cloud, mean apparent photographic magnitude 14.9. Harvard Variable number and period are indicated for each. On the right, for comparison, several galactic Cepheids (photoelectric light curves by Eggen, except, for UU Muscae, Harvard photographic light curve).

the type s light curves represent overtone pulsations (as Sandage has suggested for the very similar Eggen type c curves), must we suppose that the developing Cepheid proceeds in the direction overtone to fundamental, short to long period?

With this possibility in mind we can reexamine the amplitudes of the Magellanic Cepheids. Instead of drawing a contour diagram of mean amplitudes, we draw contour diagrams of the frequencies of amplitudes less than $0^m.7$ and greater than $1^m.0$ (Fig. 13). The picture is now greatly simplified, and suggests that the complexities of Fig. 9 are a consequence of two overlapping distributions. This possibility cannot be profitably explored further until accurate photoelectric amplitudes are available.

Finally, let us compare the frequency of periods of stars in different parts of the period-luminosity plane. The results derived from over 600 Cepheids in the Small Cloud are shown as a contour diagram in Fig. 14. The division into two groups is very evident. If, again, we suppose that a Cepheid moves from left to right across the diagram, then we can infer that its progress is not uniform.

The rate of development might be expected to be a function of the mass (i.e., the luminosity), faster for more luminous stars. It should also be a function of the time: for constant mass, log P should increase as 3/2 log R, where R is the star's radius. Thus, if the radius increased in proportion to the time, log P should in-

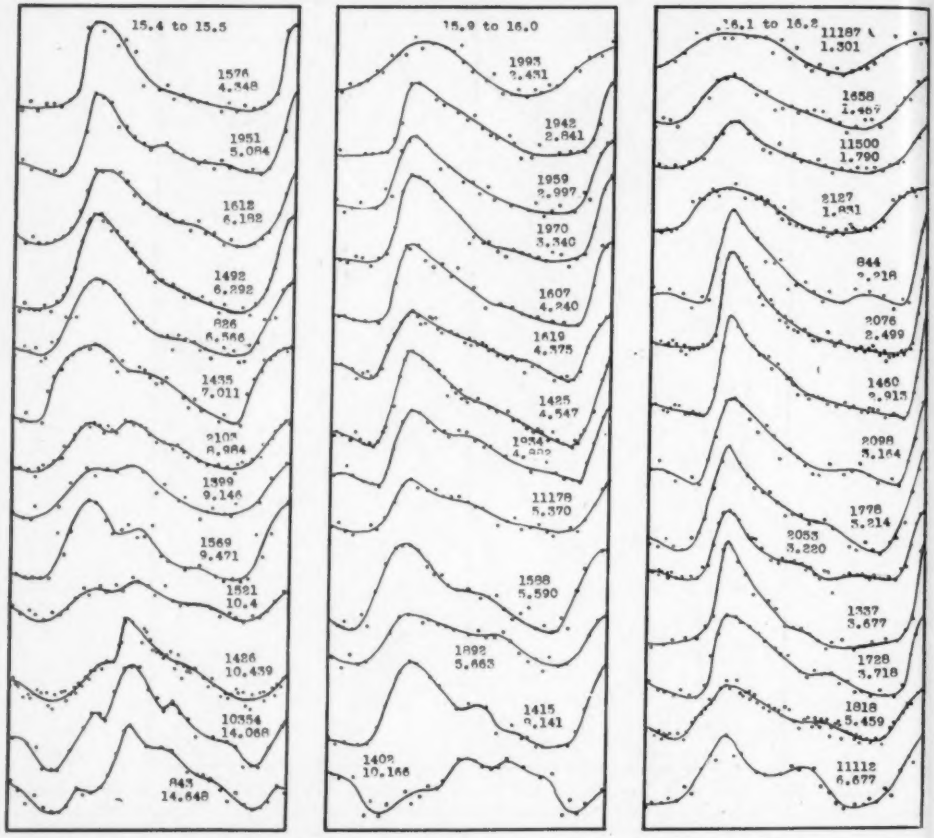

FIG. 11.—Light curves of Cepheids in the Small Magellanic Cloud, mean apparent photographic magnitudes 15.4, 15.9, and 16.1. Arrangement as in Fig. 10.

crease at an accelerated rate, and the greatest number of Cepheids at any one luminosity should occur for the shortest periods. However, it seems probable from analogy with the earlier development of massive stars, that R itself increases at an accelerated rate with time, so the concentration of Cepheids at the shortest periods would be enhanced even more. Fig. 14 is not consistent with these expectations. There are two maxima of period-frequency for all stars at and below magnitude 16. A similar situation has already been noted for the RR Lyrae stars in ω Centauri. The observations indicate that if a Cepheid moves across the period-luminosity plane, its development slows down in the neighborhood of two periods, different for each magnitude level.

If the two sets of contours refer respectively to the overtone and the fundamental, however, they also refer to different values of R at a given period. In this case, in order to convert Fig. 14 into a contour diagram representing frequency of *mean density*, we must shift the lower-period distribution to the right by an appropriate amount. If the two frequency distributions are thus combined, we obtain Fig. 15, which strongly suggests a single distribution, and also raises the question whether a given star passes through the Cepheid domain with overtone pulsation, or fundamental pulsation, or both successively. Here again we

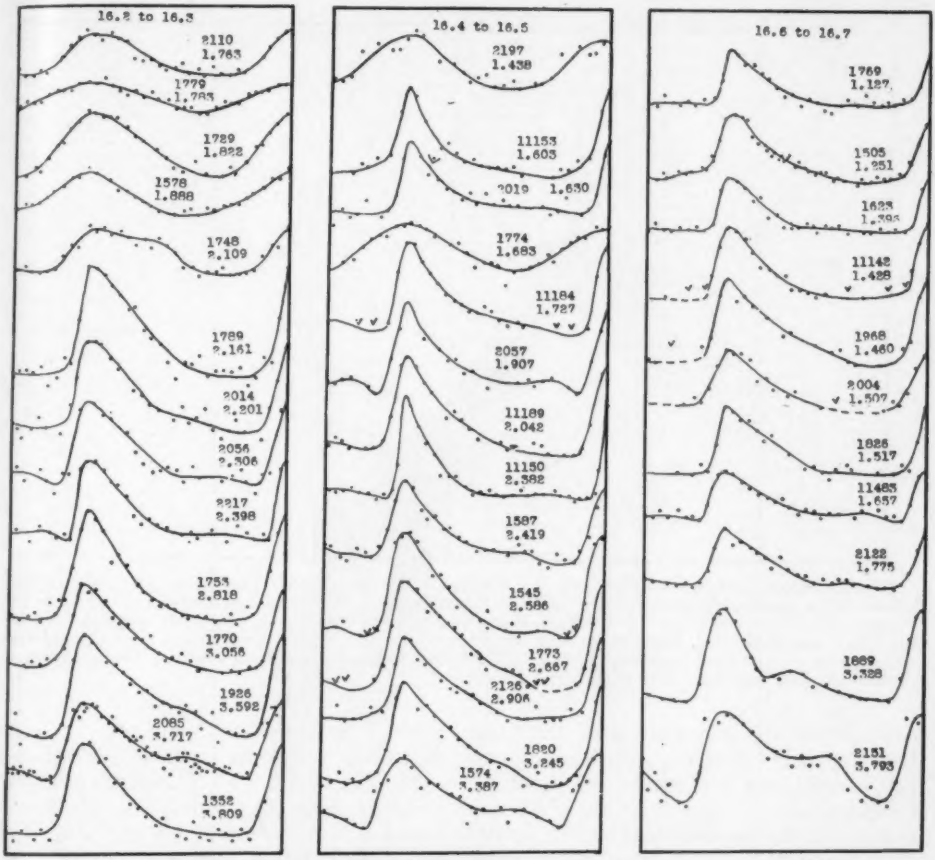

FIG. 12.—Light curves of Cepheids in the Small Magellanic Cloud, mean apparent photographic magnitudes 16.2, 16.4, and 16.6. Arrangement as in Fig. 10.

need accurate light curves and colors in order to clarify the picture. A diagram like Fig. 15 might prove to be the most fundamental representation of the relation between luminosity and mean density, and we note that its slope in the lower part is greater than that of the period-luminosity relation.

The question of the rate at which an individual Cepheid traverses the HR plane leads immediately into the wider question of the significance of the frequency of periods. The large number of Cepheids of short period in the Small Cloud, as compared with our own galaxy, has been discused by Shapley and McKibben (*40*), who regard the difference as real. Indeed, it is difficult to suppose that selection and obscuration could have cut down the numbers of galactic Cepheids with periods less than three days by a factor of ten; down to a given apparent magnitude, the Cepheids of longer period are at a greater disadvantage.

If all stars that leave the main sequence and move to the right in the HR diagram become Cepheids at some stage, we might (if their progress was uniform or followed a known law) predict the number of Cepheids per cubic parsec by means of the Salpeter "creation function." However, as we have argued above, a uniform progression does not seem to fit the known facts. We

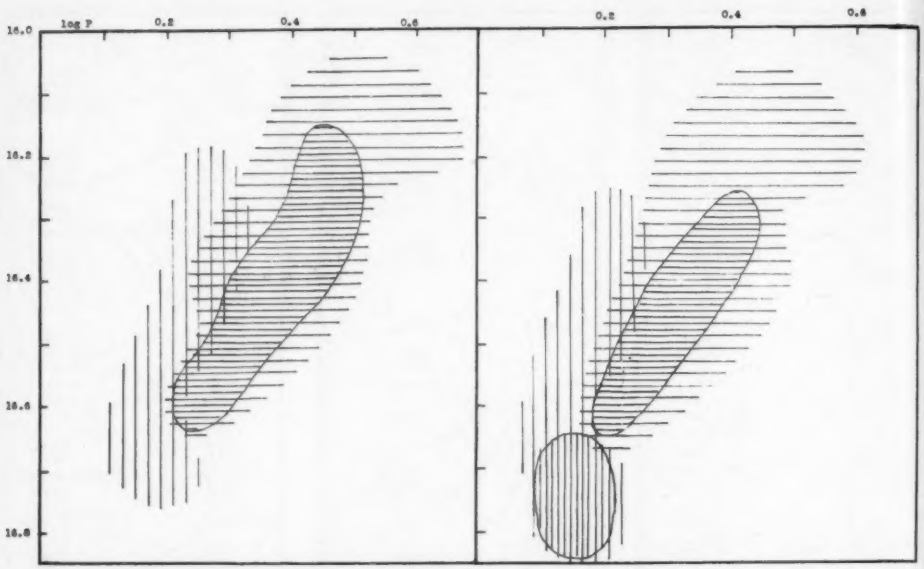

FIG. 13.—Distributions of amplitudes for Cepheids of average photographic magnitude 16.0 and fainter in the Small Magellanic Cloud. Left side: light shading, over 4 stars between limits of 0.1 in log P and in m_{pg}; heavy shading, over 6 stars. Horizontal shading: amplitude over $1^m.0$; vertical shading: amplitude less than $0^m.7$. Right side: light shading: over 6 per cent of Cepheids in given magnitude interval; heavy shading: over 10 per cent of Cepheids in given magnitude interval. Horizontal and vertical shading have the same meaning as on the left.

could invert the argument, and, assuming that Cepheids follow the period-luminosity law exactly, use the number of observed Cepheids at each period to calculate the duration of the Cepheid stage at that period. This procedure is so uncertain that I shall not presume to make a numerical application of it; it predicts an increasing number of Cepheids per cubic parsec down to periods of about a day, since all stars down to this luminosity presumably rate as massive stars, and may be thought to move nearly horizontally across the HR diagram.

However, the data can be used in another way, to examine the source of the difference between the period distribution in the Small Cloud and in our own galaxy. If the Cepheids are strictly comparable in the two systems, their rate of progress at a given absolute magnitude should be the same, and if the distribution of periods is as different as it appears to be, the only conclusion that can be drawn is that the "birth function" in the Small Cloud differs from that in our galaxy, and increases more steeply with decreasing luminosity, at least down to absolute magnitude −1.5. Information on the observed luminosity function in the Small Cloud is very indefinite, but this is an observational datum that could readily be obtained. It is possible, as Arp has suggested, that Cepheids in the Small Cloud (and, by inference, the Small Cloud itself) may differ from their galactic counterparts in chemical composition. A difference in chemical composition would, if large enough, have a noticeable effect on the mass-luminosity relation (*41*), and perhaps on the luminosity function itself.

In conclusion, I can summarize my opinion concerning the present status of the period-luminosity relation. The preliminary task of determining its average course has been completed, and we are nearing a consensus concerning the colors of Cepheids, and the relation of mean color to period. Future work must be concerned with the dispersions of the period-luminosity rela-

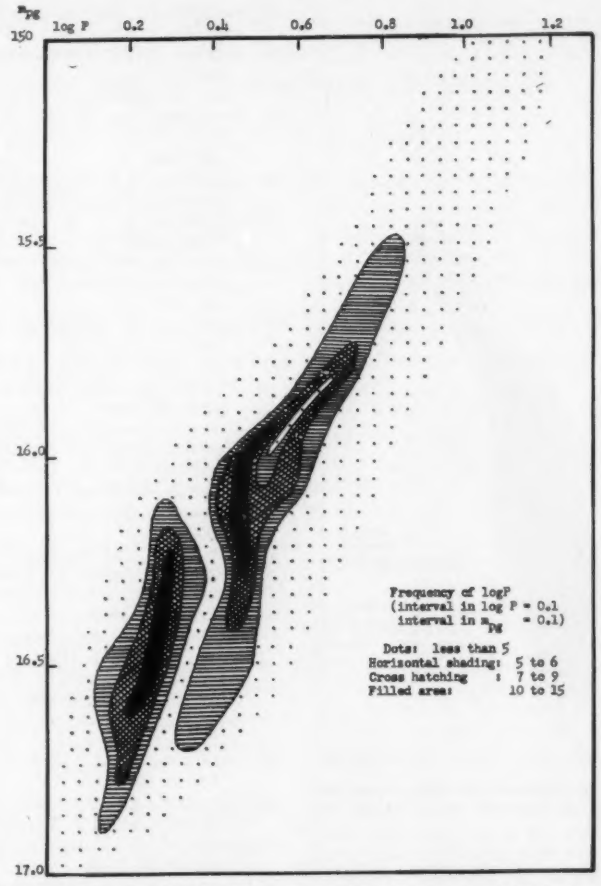

FIG. 14.—Contour diagram showing frequency of log P in the period-luminosity plane.

tion, the period-luminosity-color relation, and the period-luminosity-light curve relation. The part played by the Cepheid stage in stellar development will stimulate studies of the relation of period-frequency to the local birth function and to the rate of progress of a star through the variable stage. These last problems are intimately tied up with the study of stellar interiors, and the machine computation of evolutionary tracks. In this area, speculation is worse than valueless, and the greatest service that can be rendered by the student of variable stars is the provision of data that are accurate and complete—in other words, the systematic discovery of variable stars in carefully selected systems, accurate studies of brightness, light curve and color, and determination of luminosity functions.

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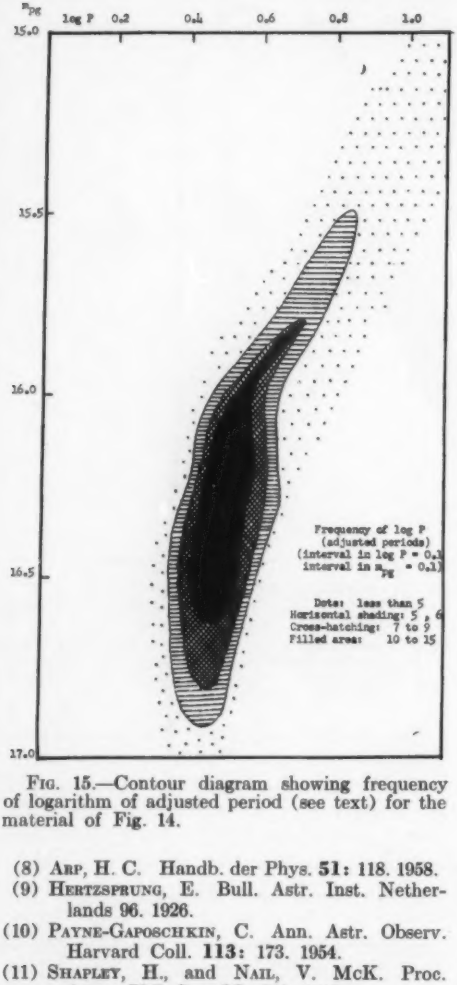

FIG. 15.—Contour diagram showing frequency of logarithm of adjusted period (see text) for the material of Fig. 14.

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PALEONTOLOGY.—*Paleontologic record of the primary differentiation in some major invertebrate groups.* DAVID NICOL, GEORGE A. DESBOROUGH, and JAMES R. SOLLIDAY, Southern Illinois University, Carbondale, Ill.

(Received July 9, 1959)

A table of the geologic ranges of the principal animal phyla, prepared by Shrock and Twenhofel (1953, p. 11), should be of interest to all students of evolution. According to their data, the animal phyla with a good fossil record, those having hard parts that are readily preserved, all appeared by about 450 million years ago, and most of them are still older. In other words, according to present knowledge of the fossil record, the major differentiation of the animal kingdom was completed by about the end of the Cambrian period. Probable exceptions to this, which would now appear to be few in number, would be of two kinds—animal phyla with poor or no fossil records and extinct phyla which are not recognized as such now. At the present state of knowledge it can be said that only many lesser groups—classes, orders, families, and genera—first appeared in time less than 450 million years ago.

This would seem to support the assertion of Willis (1940, p. 186):

> It is clear that the tests give a very strong evidence indeed in favour of the theory of differentiation or divergent mutation, according to which the course of evolution is in the opposite direction to what has hitherto been supposed, and by mutations which tend to diminish as time goes on, but go in the direction family-genus-species. The organism that first represents the family is, of course, at the same time its first genus and species, but these are of different rank from genera and species in a larger family. By further mutations this will then give rise to further genera and species. The first new genus formed will usually be widely divergent from the parent genus of the family, even if the family be quite small, e.g. of two genera only. Later formations will be less and less divergent on the whole, but will show some of the characters of divergence of their first parents. The main lines of divergence are therefore given by the latter, and later genera fill them in, as shown by a good dichotomous key.

This is the main theme in Willis's book, and he repeats it many times in various ways. In another place Willis (p. 191) states: "Evolution goes on in what one may call the downward direction from family to variety, not in the upward, required by the theory of natural selection." Willis attributes the idea of divergent mutation to H. B. Guppy and claims that it was adumbrated by St. Hilaire. More recently James Small (1951, p. 131) has stated the same idea: "The general factual picture of evolution is now one of progressive evolution by apparently large steps for the phyla, combined with diversification of genetic patterns *downwards* from phyla to families, genera, species and lower categories." Schindewolf (1951, p. 139) has stressed divergent mutation, too, as shown by this paragraph:

> Palaeontological evidence suggests that the beginning of each phylogenetic cycle, irrespective of the systematic category concerned, is marked by an intensification of evolution. In the later phases, the rate of evolution is much smaller and the ability to change decreases. An instructive example is the evolution of the placental mammals in the early Tertiary. In the upper Cretaceous the Insectivora appear, initiating the evolutionary cycle of the Eutheria. At the boundary of Cretaceous and Tertiary, and in the early Paleocene all other known placental orders become differentiated from the original group. Twenty-five orders, representing the entire morphological range of the subclass, appear in the relatively short period of 10–15 million years, whilst during the subsequent, post-Paleocene, period of 60 million years not a single new order is added.

Other workers who have favored the theory of early primary divergence could be cited, but the ones either mentioned or quoted herein should suffice to show that this is not a new idea nor is it without its adherents today. The thesis of these workers is that the major subdivisions of a group (e.g., classes of a phylum or orders of a class) generally originate early in its history, whereas new subdivisions of lesser rank (e.g., genera and species) may arise at any time throughout the group's geologic history.

For this paper the writers have taken 13 major invertebrate groups with a good paleontologic record and have recorded the

geologic ranges of their primary subgroups. In the case of a phylum, the geologic ranges of its classes were plotted; in the case of a class, the geologic ranges of its orders were recorded; and so on. With these data we hope to show whether the basic pattern of evolution is like that described by Willis and others who claim that primary divergent mutation occurs early in the history of a major group or is like that described by other workers who contend that primary divergences occur as a gradual and steady process throughout the geologic history of each group. The latter idea is conventionally considered the more logical pattern in evolution. Except for some work by Schindewolf almost no analyses of this sort have been attempted by invertebrate paleontologists.

COMPILATION AND PRESENTATION OF DATA

Thirteen examples are presented, all taken from invertebrate groups with a good fossil record. The writers have purposely avoided groups like the Trilobita and the Porifera because so much of the history of their divergence ranges back to the base of the Cambrian that a long pre-Cambrian history might be postulated for both of them even though the direct evidence of the fossil record is scanty or absent. We have avoided groups where the basic classification is not well understood or where the fossil record is rather poor. Our examples are drawn from the following phyla: Protozoa (1), Coelenterata (3), Bryozoa (1), Brachiopoda (1), Mollusca (2), Arthropoda (1), Echinodermata (3), and Protochordata (1). These, we believe, give us a reasonably large sample of the invertebrate phyla, although additional examples could have been obtained.

Another way by which we have attempted to avoid a bias of the data is to exclude the declining phase of a group's evolution—i.e., the phase in which it approaches extinction. For example, we have used only the Paleozoic history of the orders of nautiloids and the superfamilies of articulate brachiopods because the possibility of the occurrence of a primary divergence in a group approaching extinction is remote. However, in the case of the graptolites we have included data on the final stage of the group's existence because the complete geologic history, from inception to extinction, illustrates a typical pattern of rapid evolution.

The first appearance of a particular group is the most important part of the data presented here. No attempt was made to show the phylogenetic relationships of the various groups to each other, for two reasons. The first is that this information is unimportant for our purposes in this paper. Secondly, many of these relationships are not well understood and are a matter of conjecture. The writers do not claim to be experts on the phylogeny of the groups used as examples.

In the presentation of the data concerning the time of origin, only the primary divergences or largest subdivisions of a particular group have been used. In other words, for the phylum Mollusca we have considered only the classes; for the subclass Nautiloidea we have used only the orders.

We are well aware that scientists differ in their opinions concerning the classes which should be included in a particular phylum, the orders which should be included in a particular class, and, in some cases, the question of whether a certain group should be ranked as a class or an order or whether another group should be ranked as an order or a family. For this paper we have excluded aberrant groups for which the allocation is questionable and have sought to avoid excesses of classificational splitting and lumping. In deciding which primary subdivisions to include in each of our major groups we have relied on either the consensus or the latest authority. We have also done this for the data regarding the time of the first appearance of each primary subdivision, in some cases taking the majority opinion from standard textbooks on paleontology and zoology and in others using the most recent authoritative work. Only in the latter cases have we specifically cited the references from which our data were taken.

There is no exact agreement on the time

span, in millions of years, of the various periods of geologic history. We have used the same time scale as was used by Knight (1952, p. 7) with the exception of dividing the Carboniferous into Mississippian and Pennsylvanian periods and combining the Tertiary and Quaternary periods by using the Cenozoic era. Knight stated that his data were taken from *Report of the measurement of geologic time of the Division of Geology and Geography*, National Research Council, for 1949–1950, p. 18. The writers have not seen this latter reference. The chart used by Knight is here reproduced, with few modifications:

Era or period	Duration, millions of years	Occurrence, millions of years ago
Cenozoic	60	0–60
Cretaceous	70	60–130
Jurassic	25	130–155
Triassic	30	155–185
Permian	25	185–210
Pennsylvanian	25	210–235
Mississippian	30	235–265
Devonian	55	265–320
Silurian	40	320–360
Ordovician	80	360–440
Cambrian	80	440–520

DISCUSSION OF COMPILED DATA

The sequence in which the examples are presented is from the groups of organisms that are structurally simpler to the more complex ones. The first example (Fig. 1), therefore, comprises four families of planktonic Foraminifera as compiled by Loeblich and collaborators (1957). These families are generally considered by most micropaleontologists to be phylogenetically related, although there are a few planktonic Foraminifera not included in these four families. In preparing this figure the writers arbitrarily assigned the same amount of time to each of the Cretaceous stages, there being 12 of them if the Danian is excluded as was done by Loeblich and his collaborators. The first family, the Orbulinidae, appeared at the beginning of the Hauterivian stage, approximately 120 million years ago, and continues to the present. At the beginning of the Aptian stage, approximately 12 million years later, two more families emerged—the Globorotaliidae and the Hantkeninidae. These two families also have living representatives. Finally, at the beginning of the Turonian stage, the last of the families arose, the Globotruncanidae, only 30 million years after the first-appearing of these four families. The Globotruncanidae were a relatively short-lived family that became extinct at the end of the Cretaceous. To summarize: within 12 million years three of the four families made their appearance, and within approximately 30 million years all of them had emerged. Thus, all the basic differentiation took place within a time span of 30 million years and no new families have appeared in the last 90 million years.

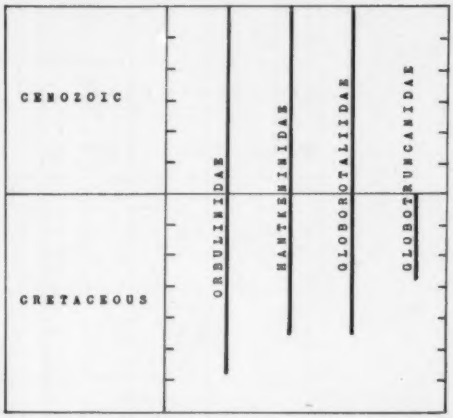

FIG. 1.—Periods of existence of four related families of planktonic Foraminifera. Data taken from Loeblich and collaborators, 1957. Horizontal stubs demark 10-million-year intervals.

The next example (Fig. 2) comprises the families of tabulate corals (data taken from Hill and Stumm *in* Moore, 1956). The first two families of the Tabulata, the Chaetetidae and Syringophyllidae, appeared almost simultaneously at the beginning of the middle Ordovician. Two more families, the Heliolitidae and Halysitidae, made their appearance during the upper part of the middle Ordovician no more than 20 million years later. At the beginning of the late Ordovician the Auloporidae and Favositidae arose; this was no more than 30 million years after the first two families of tabulate corals began their existence. Thus, in approximately 30 million years the basic di-

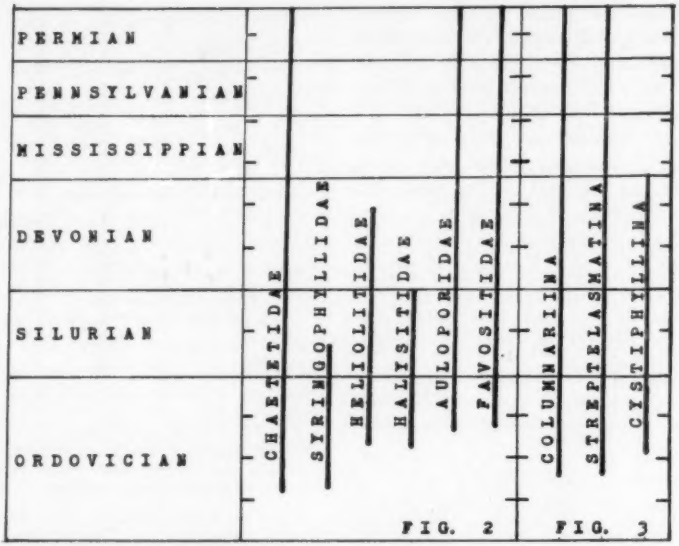

FIG. 2.—Paleozoic history of the families of tabulate corals. Data taken from Hill and Stumm *in* Moore, 1956. Horizontal stubs demark 20-million-year intervals.
FIG. 3.—Periods of existence of the suborders of rugose corals. Data taken from Hill *in* Moore, 1956. Horizontal stubs demark 20-million-year intervals.

vergence of the Tabulata was completed, and no new families appeared throughout the remaining 200 million years of the Paleozoic era.

Many of the major groups studied have included subgroups which existed only briefly, usually early in the history of the major group. For example, the Syringophyllidae, Heliolitidae, and Halysitidae appeared within the first 20 million years of tabulate existence. The Syringophyllidae were extant for about 70 million years, the Heliolitidae for less than 120 million years, and the Halysitidae for about 80 million years. The occurrence of short-lived subgroups is common enough that it should be considered an important phenomenon, although it has been left unexplained in theories on the basic causes of evolution.

The suborders of the rugose corals (Fig. 3) (data taken from Hill *in* Moore, 1956) provide another illustrative example of rapid primary divergence. All three suborders of the Rugosa emerged within about the first 10 million years of the order's beginning in the middle Ordovician. No new suborders appeared during the remainder of the Paleozoic, a span of 220 million years, although many families and groups of lesser rank did arise after all of the suborders had been established.

Another interesting example (Fig. 4) is that of the primary divergence in the scleractinian corals (data taken from Wells *in* Moore, 1956). Three of the five suborders appeared almost simultaneously in the middle Triassic. About 25 million years later the fourth suborder arose in the early Jurassic. Some 80 million years after that, or about 105 million years after the scleractinians began, the last suborder originated in the late Cretaceous. No new suborders have appeared during the 70 million years since. Most of the basic divergence in the scleractinian corals took place within the first 25 million years, and only one new suborder appeared in the last 150 million years of scleractinian history.

Many scientists, particularly in the field of genetics, would expect evolution to be a

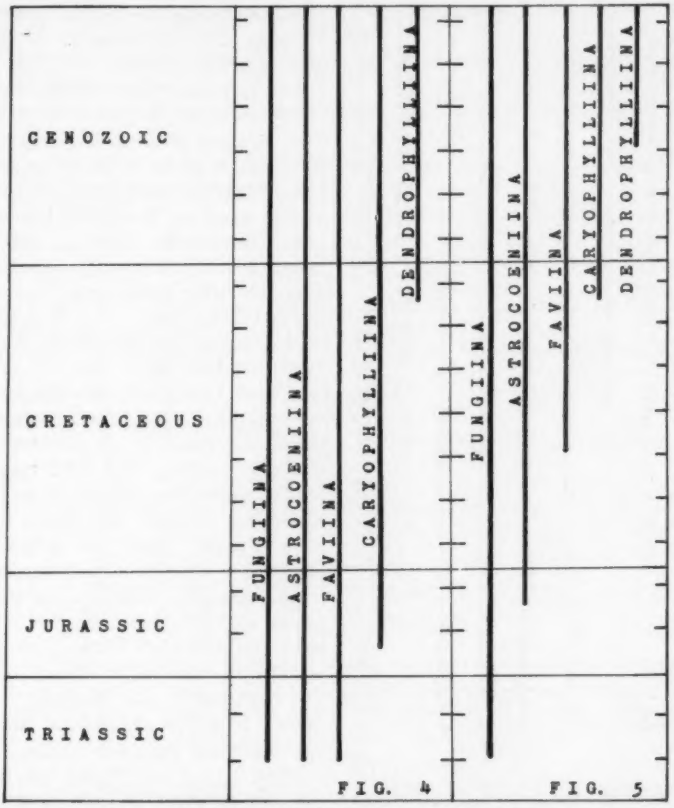

FIG. 4.—Periods of existence of suborders of scleractinian corals. Data taken from Wells *in* Moore, 1956. Horizontal stubs demark 10-million-year intervals.

FIG. 5.—Hypothetical periods of existence of suborders of scleractinian corals. If evolution were a slow, gradual, and steady process, with primary divergences occurring at regular intervals throughout geologic history, new suborders of scleractinian corals would have arisen at 35-million-year intervals. Cf. Fig. 4.

relatively steady and gradual process, with primary divergences occurring one by one at regular intervals throughout the history of a major group. We digress here in order to compare the actual paleontologic record of the suborders of the scleractinian corals with the theoretical record which would have been established if this hypothesis were true (cf. Figs. 4 and 5). Assuming that the scleractinian corals have existed for 175 million years, the first suborder having originated at the beginning of the middle Triassic, one might expect the other four suborders to appear thereafter one at a time at 35-million-year intervals (and a new suborder would be due to arise soon). Thus, according to the "regular interval" theory, one suborder would have originated at the base of the middle Triassic, one in the middle Jurassic, one in the early middle Cretaceous, one in the late Cretaceous, and one near the middle Cenozoic. In actual fact, however, the record is remarkably different.

It should be pointed out that the foregoing comparative example is based on a group that evinces little or no indication of decline in evolutionary vigor at the present time. Similar comparisons between actual and theoretical evolution are presented in

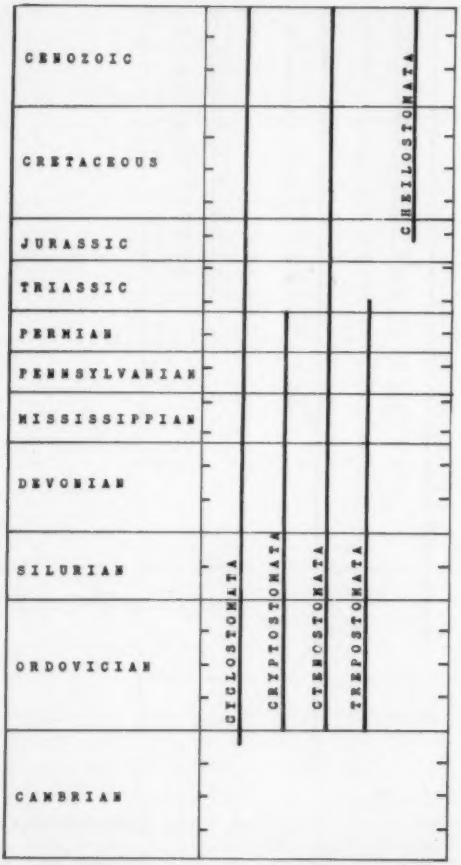

FIG. 6.—Periods of existence of classes of Bryozoa. Horizontal stubs demark 20-million-year intervals.

Figs. 8 and 9, the classes of the Mollusca, and Figs. 12 and 13, the classes of the Echinodermata. These phyla also show no tendency toward extinction at the present time. In all three examples it is clear that major divergences have not occurred gradually or at regular intervals throughout the history of each group.

Returning to the presentation of the basic data, we cite another good case of early rapid divergence: the five classes of the phylum Bryozoa (Fig. 6). Within probably 10 million years during late Cambrian and early Ordovician times, four of the five classes appeared. Not until 310 million years later did the fifth class, the Cheilostomata, make its debut during the late Jurassic. No new classes of the Bryozoa have appeared within the past 140 million years. In other words, most of the basic divergence in the Bryozoa occurred during a brief span of 10 million years; for the past 450 million years, little primary divergence has occurred within the phylum.

The superfamilies of the Paleozoic articulate brachiopods (Fig. 7) also provide a good example of rapid primary divergence. The data were taken from Cooper and Williams (1952, part of fig. 6, p. 332). At the beginning of the Cambrian the Orthacea emerged. No more than 20 million years later, still in the early Cambrian, three more superfamilies began their existence. Two of these, the Rustellacea and the Kutorginacea, were short-lived and became extinct within about 35 million years. Then there was a lag of nearly 80 million years, or 100 million years after the beginning of the Cambrian, before more divergent mutation took place. The Triplesiacea and the Atrypacea appeared almost simultaneously in the middle of early Ordovician time. About 10 million years later two more superfamilies emerged in the late early Ordovician. Some 15 million years after that, five more superfamilies appeared; this was accomplished by middle Ordovician time. During the late Ordovician one more superfamily arrived on the scene, the Productacea. Thus, within a part of the Ordovician period spanning less than 60 million years, 10 new superfamilies appeared. By the middle part of the early Silurian the last two superfamilies began their existence. It took more than 170 million years for all 16 of the superfamilies to emerge. In the remaining 165 million years of the Paleozoic era, no new superfamilies of articulate brachiopods appeared, and, with one possible exception, none arose during the articulate brachiopods' period of decline in evolutionary vigor, the 185 million years represented by the Mesozoic and Cenozoic eras.

The time lag of 80 to 100 million years between the appearance of the first articulate brachiopod superfamilies and the time of rapid divergence which began in the early Ordovician is analogous to the time lag between the inception and the period of rapid

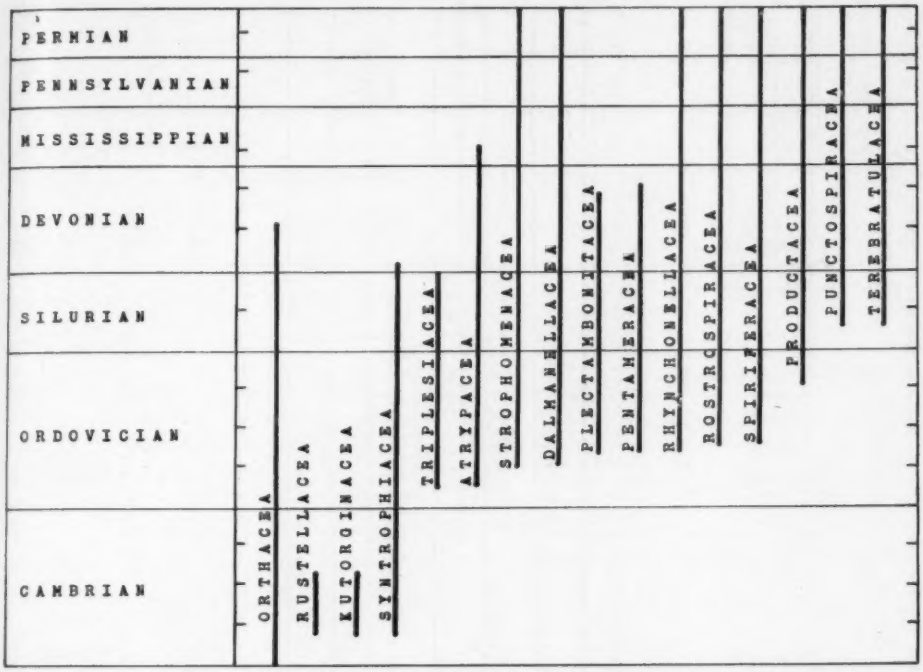

FIG. 7.—Paleozoic history of superfamilies of articulate brachiopods. Data taken from Cooper and Williams, 1952, part of fig. 6, p. 332. Horizontal stubs demark 20-million-year intervals.

emergence of the mammalian orders. As in the case of the mammals, the postponement of rapid divergence of the articulate brachiopods may have been due in part to competition from another group—in this instance the inarticulate brachiopods which flourished first. Another possibility is that the Cambrian seas may have been more suitable for animals with chitinophosphatic shells (e.g., most, but not all, of the inarticulate brachiopods), whereas a favorable environment for animals with calcareous shells (e.g., the articulate brachiopods) did not develop until later. This possibility seems to be confirmed by the fact that many calcareous-shelled animals originated in the early and middle Ordovician (Raymond, 1939, p. 42); examples are the pelecypods, the rugose and tabulate corals, and the bryozoans. Possibly these two factors together may have caused the postponement of rapid primary divergence of the articulate brachiopods.

The classes of the Mollusca (Fig. 8) originated early in the history of the phylum. The gastropods began at the base of the Cambrian. About 60 million years later, in the late Cambrian, the Cephalopoda and the Amphineura appeared. Twenty million years after this latter event, at the beginning of the Ordovician, the Pelecypoda began their existence. Finally, the Scaphopoda emerged at the base of the Silurian, 160 million years after the beginning of the Cambrian, or 80 million years after the appearance of the Pelecypoda. No new classes of Mollusca have emerged during the 360 million years since the beginning of the Silurian. In other words, most of the primary divergence within the Mollusca was accomplished in no more than 80 million years, and it all occurred within a span of 160 million years. All the known classes of the Mollusca are long-lived.

Once again the authors digress, this time to compare the actual history of the ap-

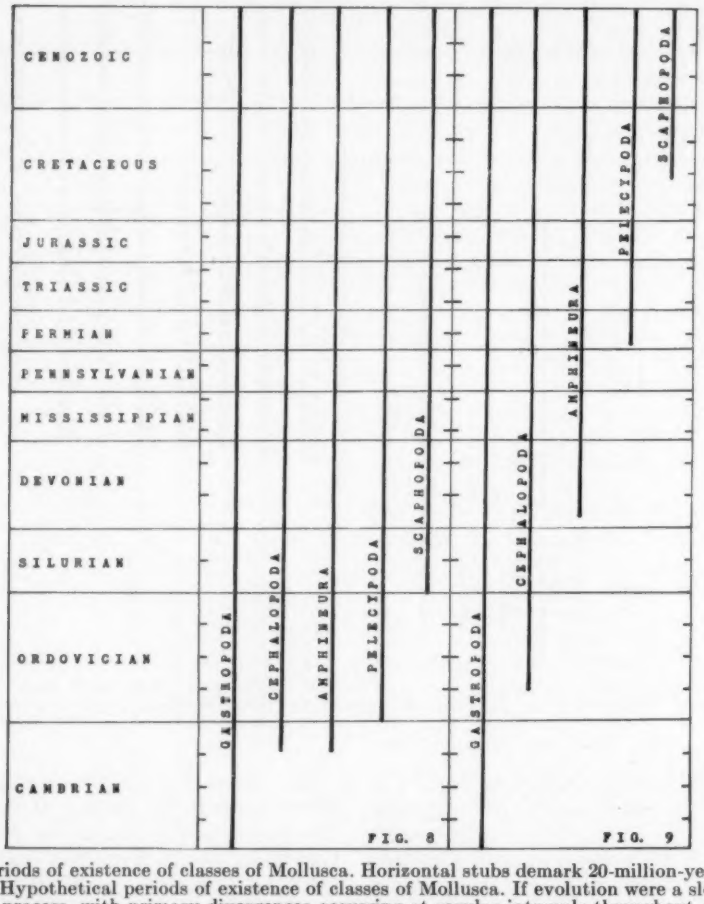

FIG. 8.—Periods of existence of classes of Mollusca. Horizontal stubs demark 20-million-year intervals.
FIG. 9.—Hypothetical periods of existence of classes of Mollusca. If evolution were a slow, gradual, and steady process, with primary divergences occurring at regular intervals throughout geologic history, new classes of Mollusca would have arisen at 104-million-year intervals. Cf. Fig. 8.

pearance of the molluscan classes, based on the paleontologic record, with a hypothetical sequence of divergences based on the idea that the classes should appear at approximately regular intervals throughout the entire history of the phylum. If the time from Cambrian to Recent is taken as 520 million years and the first class originated at the base of the Cambrian, then the next four classes should have emerged one by one at approximately 104-million-year intervals and a new, or sixth, class could be expected to appear soon. Accordingly, one class should have arisen at the beginning of the Cambrian, the next one in the early middle Ordovician, the third near the beginning of the Devonian, another at about the base of the Permian, and the last known one in the middle Cretaceous. That the actual record is sharply different from the hypothetical is illustrated by a comparison of Figs. 8 and 9.

Another case of early rapid divergence (Fig. 10) is seen in the orders of the nautiloids (data taken from Flower and Kummel, 1950, with slight modifications). During the late Cambrian the first order of nautiloids, the Ellesmeroceratida, appeared. Beginning at the base of the Ordovician and extending to the middle Ordovician, a tremendous

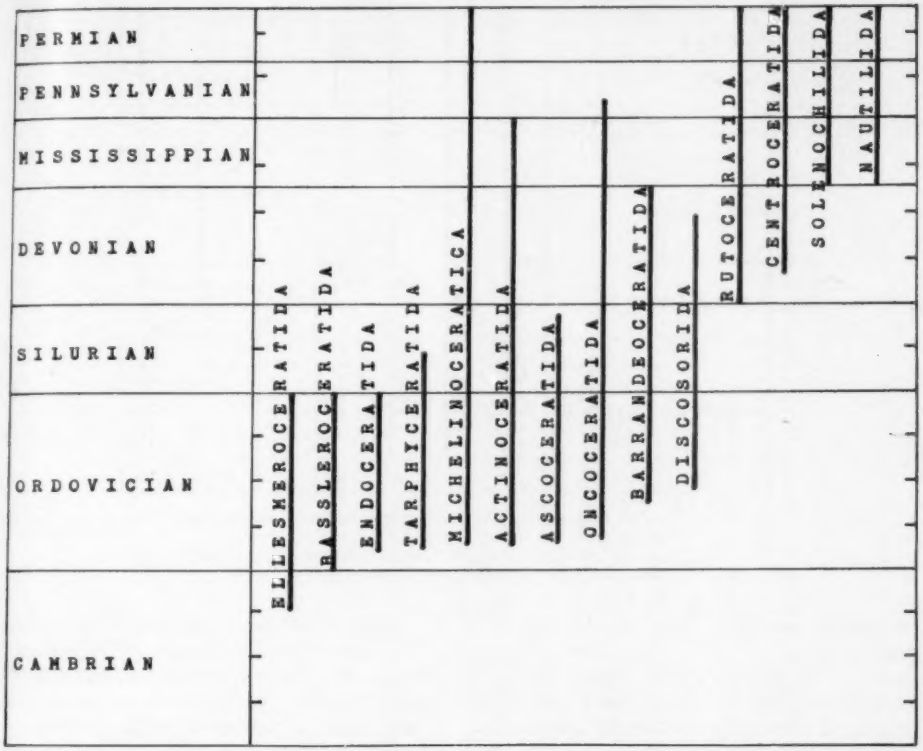

FIG. 10.—Paleozoic history of orders of nautiloid cephalopods. Data taken from Flower and Kummel, 1950, with slight modifications. Horizontal stubs demark 20-million-year intervals.

burst of divergent mutation occurred: within a span of no more than 40 million years, and within about 60 million years of the first appearance of the nautiloids, nine new orders emerged. Several of these were relatively short-lived, having existed for about 100 million years and in a few cases even less. Between 80 and 90 million years later, in the early Devonian, two more orders appeared. Finally, the last two orders arose in the early Mississippian about 195 million years after the beginning of nautiloid history. No new orders of nautiloids emerged during the final 80 million years of the Paleozoic, nor did any appear during the Mesozoic and Cenozoic eras when the general trend of the nautiloids was toward extinction. It is noteworthy that five-sevenths of the nautiloid orders originated within the first one-seventh of the nautiloids' period of existence. In other words, most of the major groups (10 of 14) appeared between the late Cambrian and middle Ordovician. This corresponds well with the time of rapid divergence of many other organisms that had calcareous shells. In the last 400 million years of nautiloid history only four new orders emerged, and even they all began within the first 135 million years of that span of time.

The first superfamily of Paleozoic ostracodes (Fig. 11) emerged at the beginning of the Ordovician period. In the early Ordovician, also, and about 15 million years later, two more superfamilies appeared. About 190 million years after that, the fourth and last superfamily originated; this was at the base of the Pennsylvanian period. During the remainder of the Paleozoic era, 50 million years, no new superfamilies of

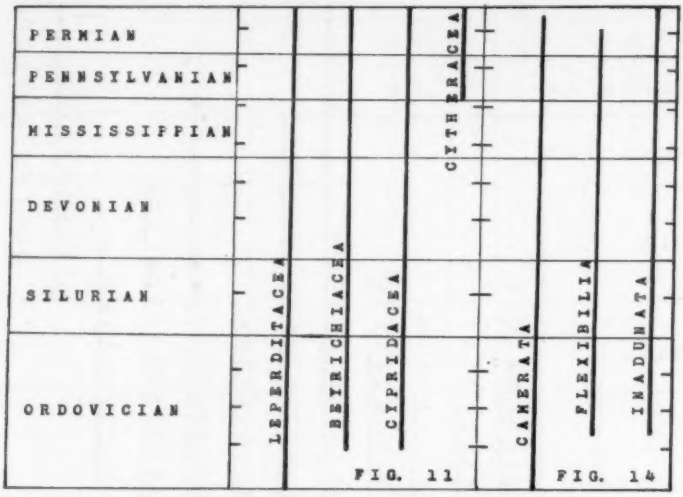

FIG. 11.—Paleozoic history of four superfamilies of ostracodes. Horizontal stubs demark 20-million-year intervals.
FIG. 14.—Paleozoic history of three subclasses of crinoids. Horizontal stubs demark 20-million-year intervals.

ostracodes emerged. Thus, three of the four major groups of ostracodes arose within a span of 15 million years during the early Ordovician, and only one new superfamily appeared during the remaining 240 million years of the Paleozoic era.

In regard to early divergent mutation, perhaps the most illustrative and interesting group studied comprises the classes of the phylum Echinodermata (Fig. 12). The data, collated from several different sources, represent a concensus of authorities. A few questionable groups were not included, as for instance the Bothriocidaroida, which is considered a separate class by Moore (Moore, Lalicker, and Fischer, 1952, p. 577) but not by others, and the classes Cyamoidea and Cycloidea, which are aberrant short-lived middle Cambrian groups and are discussed only by Shrock and Twenhofel (1953, pp. 694–696). If these groups had been included in the present study, the depiction of early divergent mutation among the echinoderms would have been even more striking.

Near the beginning of the Cambrian the Edrioasteroidea appeared, and about 25 million years later, in the middle Cambrian, the Eocrinoidea made their debut. Also in the middle Cambrian, and about 10 million years after the appearance of the Eocrinoidea, the Carpoidea emerged. For the remainder of the Cambrian, about 40 million years, no new classes of echinoderms appeared. At the beginning of the Ordovician, however, three more classes arose. Within the next 40 million years, and no later than middle Ordovician, the Paracrinoidea, Cystoidea, Echinoidea, and Blastoidea made their debut. The Holothuroidea originated in the middle Devonian, no more than 110 million years later than the middle Ordovician. No new classes appeared after the middle Devonian, or for the past 290 million years. Except for the holothuroids, all the classes of echinoderms emerged within the first 120 million years (roughly the first quarter) of the history of the phylum. The most rapid divergence took place within the first 40 million years of the Ordovician period, coinciding again with the time of rapid divergent mutation of many major groups of animals with calcareous skeletons. It is interesting to note here that several of the echinoderm classes were short-lived, having originated and expired early in the history of the phylum.

The writers have chosen the classes of the

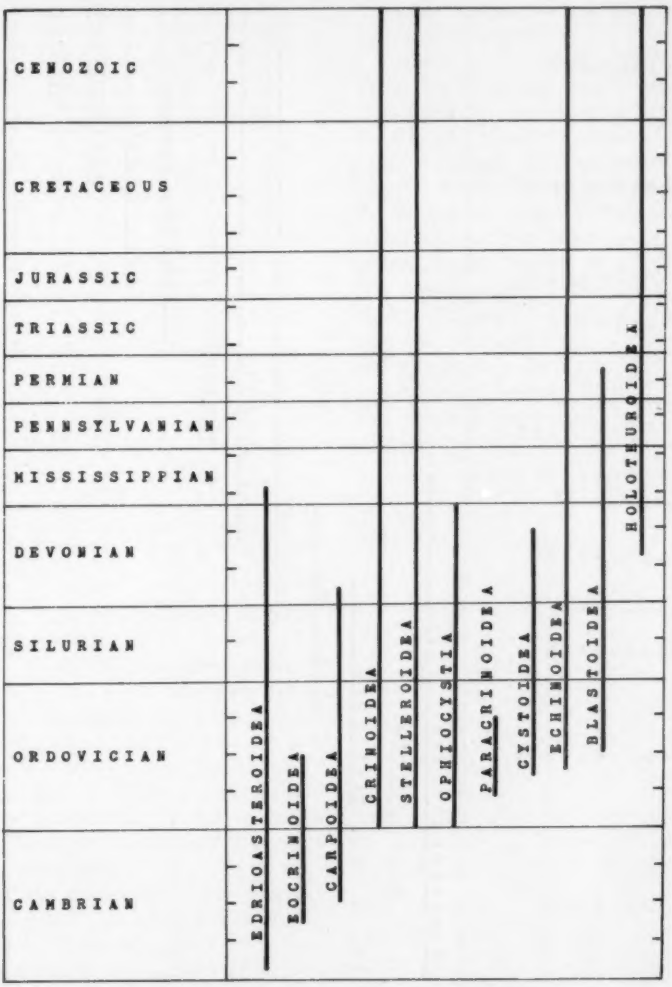

FIG. 12.—Periods of existence of classes of Echinodermata. Horizontal stubs demark 20-million-year intervals.

phylum Echinodermata, a group that shows no evidence of becoming extinct, for presentation of another example of the difference between the actual and hypothetical records of primary differentiation. If we assume that the phylum's history from early Cambrian to Recent spans 520 million years and if we theorize that evolution is a relatively steady and gradual process, the 11 classes of echinoderms should have originated one by one at about 47-million-year intervals. Hence, their individual emergences should have occurred in the (1) base of the Cambrian, (2) middle Cambrian, (3) early Ordovician, (4) late Ordovician, (5) late Silurian, (6) late middle Devonian, (7) latest Mississippian, (8) late Permian, (9) middle Jurassic, (10) middle Cretaceous, and (11) early Cenozoic. The theory appears fallacious, however, when one examines the actual record, which shows that three classes originated before the Ordovi-

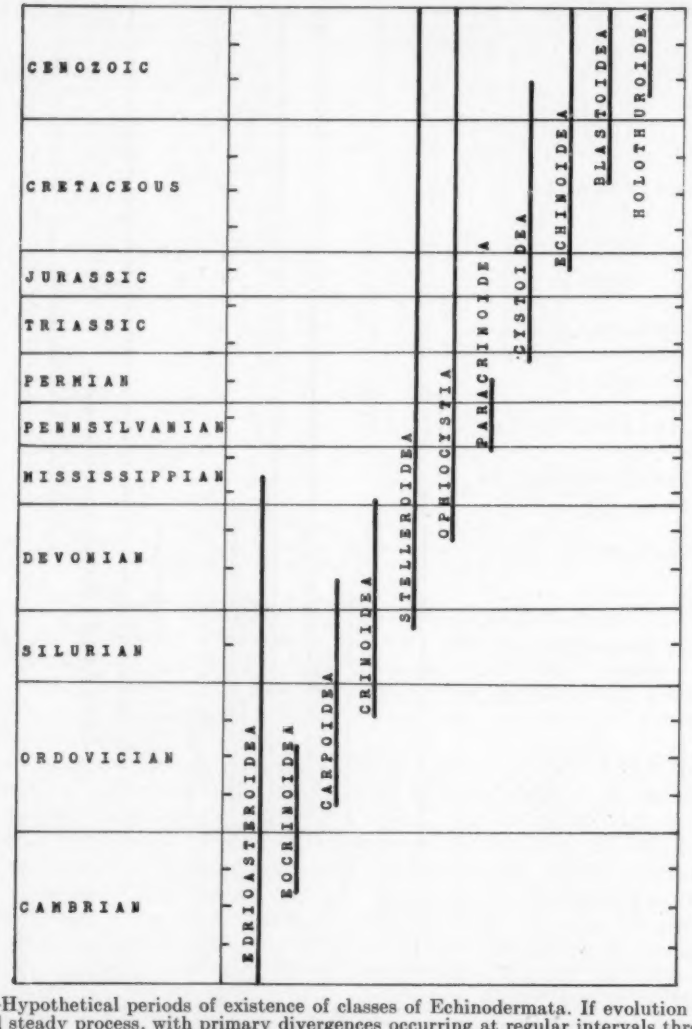

FIG. 13.—Hypothetical periods of existence of classes of Echinodermata. If evolution were a slow, gradual, and steady process, with primary divergences occurring at regular intervals throughout geologic history, new classes of Echinodermata would have arisen at 47-million-year intervals. Horizontal stubs demark 20-million-year intervals. Cf. Fig. 12.

cian, seven during the Ordovician, and only one thereafter. To facilitate comparison we present the actual and theoretical records in Figs. 12 and 13.

The first subclass of Paleozoic crinoids (Fig. 14), the Camerata, appeared at or near the beginning of the Ordovician. No more than 30 million years later, in the early middle Ordovician, the other two subclasses made their debut. Once again we see the early and middle Ordovician as a period of rapid emergence of animals having calcareous shells. For the remainder of Paleozoic time, about 225 million years, no new subclasses of crinoids arose.

The orders of the irregular echinoids are an excellent case of adaptive radiation and rapid divergent mutation (Fig. 15). As soon as the echinoids developed the ability to thrive on a sandy or muddy substrate, they

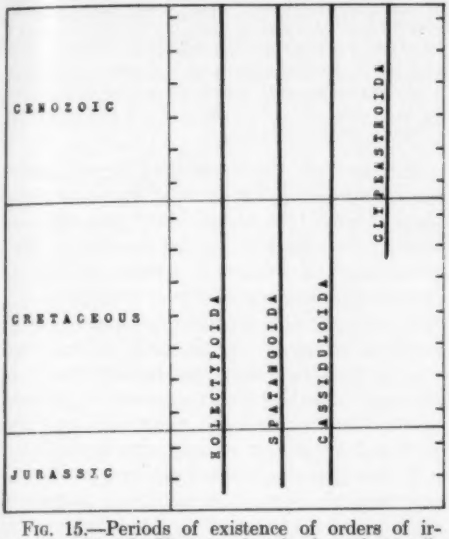

FIG. 15.—Periods of existence of orders of irregular echinoids. Horizontal stubs demark 10-million-year intervals.

evolved quickly. The first order, Holectypoida, appeared in the early Jurassic. Two more orders sprang into existence almost simultaneously in the early Jurassic, probably no more than two million years later. The last order, the Clypeastroida, did not emerge until the late Cretaceous, about 70 million years later. For the past 80 million years no new orders of irregular echinoids have arisen. Most of the primary divergent mutation occurred within the first two million years of the existence of the irregular echinoids; only one new order arose during the subsequent 150 million years.

The five orders of graptolites (Fig. 16) give an excellent and typical picture of the entire history, from inception to extinction, of a rapidly evolving group of organisms. The Dendroidea appeared first in the middle Cambrian. About 25 million years later, in the late Cambrian, the Graptoloidea arose; and approximately 10 million years after that, at the beginning of the Ordovician period, the other three orders began their existence. Two of the latter three orders were short-lived, existing for less than 30 million years. All of the basic divergence within the graptolites was accomplished in about 35 million years. In the remaining 185 million years of graptolite existence, no new orders appeared.

The history of the graptolites can be divided into three phases such as Schindewolf (1951, p. 139) has depicted for other groups of animals. The first phase of rapid divergent evolution (typogenesis) occurred in the graptolites from middle Cambrian to the beginning of the Ordovician—approximately 35 million years—and was characterized by the origin of all of the orders. The second phase (typostasis), or the acme of development of graptolites from the standpoint of numbers of families, genera, and species, occurred during the Ordovician and Silurian periods, or in about 120 million years. This second phase was marked not only by the origins of new families, gen-

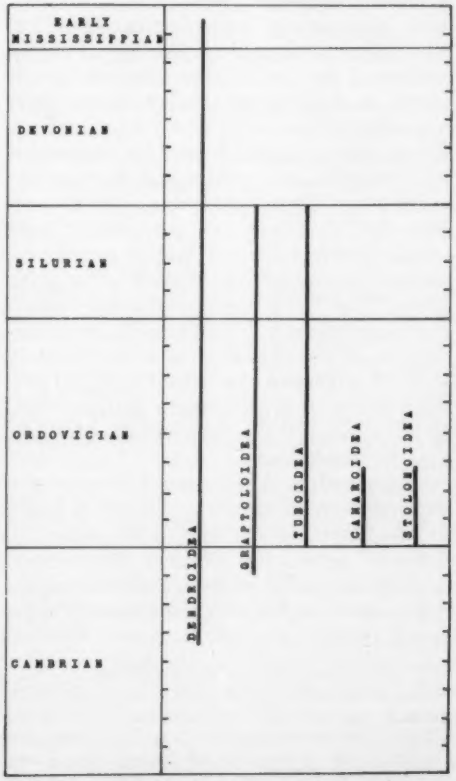

FIG. 16.—Periods of existence of orders of graptolites. Horizontal stubs demark 10-million-year intervals.

era, and species but by the extinction of others. Finally, in the third phase (typolysis) the numbers of lesser subgroups declined and the graptolites became extinct. This last phase occurred during the Devonian and early Mississippian and spanned 65 million years. The senior author (1954, p. 24) has shown that a similar cycle of development, on a much smaller scale, occurred in the long-lived pelecypod species *Glycymeris americana* with regard to its populations and variations.

INFERENCES AND CONCLUSIONS

Believing that the 13 examples used in this study are representative of major invertebrate groups, the authors observe that primary divergent mutation typically occurs early in a group's history, as diagrammed by Schindewolf (1950, p. 239). Thus, the origin of a phylum is closely followed by the origin of all its classes; the inception of a class is soon followed by the inception of all its orders; and a new order is quickly completed in terms of its families. An occasional major divergence may occur much later than the others, but this is rather exceptional. These observations are at variance with the theory that primary differentiation occurs gradually and at regular intervals throughout the history of a given group. That the latter contention is fallacious is graphically demonstrated by a comparison of Fig. 4 with 5, 8 with 9, and 12 with 13, depicting the actual and theoretical histories of the suborders of the scleractinian corals and the classes of the Mollusca and Echinodermata.

One possible explanation for early primary divergent mutation within a major group of animals is alluded to in a somewhat different aspect by Simpson, Pittendrigh, and Tiffany (1957, p. 588). In discussing the appearance of the amphibians they have this to say:

> It is characteristic of evolution that the amphibians did not evolve from late, specialized, progressive or perfected osteichthyans, such as the teleosts, but from primitive forms that lived near the beginning of osteichthyan history. It has usually been true that when a radical adaptive change occurs and a new major group arises, it originates from primitive and not from advanced members of the ancestral group. With progressive adaptation to any one way of life, there often comes a time when the adaptation seems to become irrevocable—a special aspect of the irrevocability of evolution in general. Then change to a radically different way of life becomes, if not impossible, at least extremely improbable.

For example, suppose that the Cephalopoda arose from the Gastropoda: this must have occurred, if at all, early in gastropod history, while the gastropods were still primitive and relatively unspecialized, because later representatives of a major group are generally too specialized to give rise to another group of equal rank. The actual case is that the Cephalopoda did emerge in the first one-eighth of gastropod history, during the time that the gastropods still had primitive or unspecialized representatives.

A fairly common phenomenon is the occurrence of aberrant short-lived subgroups such as two orders of graptolites, several classes of echinoderms, three families of tabulate corals, several superfamilies of articulate brachiopods, and several orders of nautiloids. In most, but not all, cases these short-lived subgroups were among the earlier divergences of their respective groups. If the taxonomic rank assigned to these subgroups is correct on the basis of morphology, then several interesting inferences can be drawn. First: knowing that extinction of families, orders, and classes is not uncommon, one might reasonably assume that extinction of phyla is also not uncommon. The type of geologic history could be the same, in which case extinct phyla may well be more numerous than paleontologists have heretofore acknowledged. Thus, when dealing with aberrant groups which can be only doubtfully allocated to extant phyla, perhaps taxonomists would be more accurate in assuming that they represent extinct phyla. With little confidence and less evidence, paleontologists have allocated aberrant groups such as the conulariids, stromatoporoids, labechiids, receptaculitids, and pleosponges to phyla which still have living representatives; but the fossil groups are sufficiently different from modern groups that such allocations may be erroneous and the extinct groups may actually represent extinct phyla.

It should be stressed, however, that not all extinct groups do represent extinct phyla, no matter how difficult their proper allocations to extant phyla may be. A class of fossil animals having structurally simple hard parts may be so lacking in distinctiveness that its phyletic assignment is dubious; and yet, if the soft parts were available for examination, all doubt would be removed. Moore (Moore, Lalicker, and Fischer, 1952) makes an excellent point when he states (pp. 273–274): "The scaphopods hold unquestioned status as members of the Mollusca in good standing, but if they were known only as fossils, it is certain that they would be put on an *incertae sedis* (uncertain classification) list."

Let us further explore the possibility that extinct phyla may be fairly numerous. The extinction of a phylum of course implies the extinction of all its classes. Conversely, the survival of other phyla implies the survival of at least some of their classes and occasionally the inception of new classes. Considering extinctions, survivals, and new inceptions, one is led to wonder whether there were more phyla and classes of living invertebrates at any one time in the past than there are today. In the case of the echinoderm and bryozoan classes, to cite but two examples, there is no doubt. One has only to look at Figs. 6 and 12 to see that these phyla had more classes of living representatives in the Paleozoic era than in the present. Yet these phyla do not appear to be approaching extinction. That is to say, despite a net reduction in the number of classes, the echinoderms and bryozoans are still flourishing and may actually have more genera and species today than at any other moment of history.

Although they may represent fewer classes and phyla, we would be inclined to believe that there are as many species, genera, families, and possibly orders of animals and plants living on the earth today as at any specific time in the geological past. When one considers the ecological relationships among plants and animals, one realizes that the appearance of a new species generally provides another ecological niche or habitat for one or more additional species as commensals, symbionts, or parasites. The development of grasses provided impetus to the evolution of mammals; the origin of flowering plants promoted the development of insects; more fundamentally, the emergence of land plants was followed by rapid evolution of terrestrial animals. Furthermore, most non-parasitic animals have parasites living inside or outside their bodies, and many of the parasites are peculiar to one or, at most, a few species of host; and so the origin of a new host species encourages the origin of new parasites. Of course, it follows that the extinction of a species may lead to the extinction of some or all of its commensals, symbionts, and parasites; but we strongly suspect that in the general trend of geologic history the proliferation of some genera has fully offset the decline of others. Accordingly, while there may have been a net decline in the number of major living groups (phyla and classes), there has probably been no net decline in the number of minor living groups (genera and species).

Commenting on extinctions, survivals, and new inceptions of major and minor groups, Simpson, Pittendrigh, and Tiffany (1957, p. 754) state:

> Since the Ordovician innumerable groups have died out, but as they disappeared their places were simply taken over by other groups, generally of more recent origin. Among animals and animal-like protists that are at all likely to leave a fossil record, there are only 12 phyla and 31 classes in the present seas. That actually represents a slight decrease from the 13 phyla and 33 classes known for late Ordovician seas. The recent phyla are the same as those of the Ordovician. Several of the classes are of later origin and have replaced extinct classes present in the Ordovician. Replacement has been more and more complete at lower levels of the hierarchy of classification.

Why have some of the major groups become extinct? In assembling the data for this paper we have observed the following facts. It seems that several different basic patterns of morphology arose among the groups which, early in their history, had a number of short-lived primary subgroups, as for example the classes of the Echinodermata and the orders of the Nautiloidea. In each case, the "successful" pattern of mor-

phology was exhibited only by the long-lived subgroups and was characterized by the development of numerous genera and species flourishing over a wide geographic area for a long period of time. Once the basic pattern had been established, subsequent modifications were relatively minor but numerous. In contrast, the basic morphologic patterns adopted by the short-lived subgroups (and a few of the long-lived ones) exhibited very few minor modifications and never became "successful" in the sense of being characterized by large numbers of genera and species and broad geographic range.

Completing our summary, we call attention to the fact that many groups of animals with calcareous skeletons show primary divergence most rapidly during the latest Cambrian and early and middle Ordovician. Exemplifying this phenomenon are the echinoderms, the tabulate and rugose corals, the bryozoans, the articulate brachiopods, the mollusks, the nautiloids, and the Paleozoic crinoids. Raymond (1939, pp. 34, 38–40, 42) noted that the Ordovician was a period of rapid development and evolution of calcareous-shelled animals, and our data confirm his assertions.

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BOTANY.—*The Danthonia-Lichen-Moss community in Washington, D.C., and vicinity.* Sister JULIA MARIE VAN DENACK and HERBERT C. HANSON, Catholic University of America.

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The purpose of this paper is to describe a Danthonia-Lichen-Moss community as it exists in Washington, D.C., and vicinity and to discuss its possible role in ecological succession. This community, heretofore undescribed, is ecologically interesting as it seems to be confined to disturbed places and is found in woodland clearings, along the periphery of woods, and on eroding areas. It consists chiefly of the poverty oat-grass, *Danthonia spicata*,[1] the lichens, *Cladonia cristatella* and *C. subtenuis*, and a variety of mosses.

PROCEDURE

Six stands of the Danthonia-Lichen-Moss community in different locations in and near Washington, D.C., were analyzed during March and April 1959. The greatest distance between stands was 7 miles.

The vegetation was analyzed by means of 2-decimeter-square quadrats placed at regular intervals through the center of each stand (except in stand 3 where intense erosion and degradation of the community necessitated selection of quadrat areas for study). Ten quadrat samples were studied in each of the six stands. Cover estimates of the vegetation were made using the Hult-Sernander scale modified by Hanson (1953) where a cover of 6 is assigned a species with vertical projection of its living parts covering 3/4 to 4/4 of the quadrat, 5—1/2 to 3/4, 4—1/4 to 1/2, 3—1/8 to 1/4, 2—1/8 to 1/16, 1—less than 1/16, x—rare, vitality low. From tabulated data on each stand the average cover and per cent constancy of each species were computed (see Table 1).

Soil samples from 0 to 1 inch and 1 inch to 3 inch depths were taken and analyzed for texture by the Bouyoucos (1951) hydrometer method, pH according to the colorometric system using bromcresol green indicator, and color designation with the Munsell color charts (Soil Survey Staff, 1951).

[1] Nomenclature follows Gleason (1952).

The first study area was located on the west side of U.S. Highway No. 1 on top of a hill south of the business section in University Park, Md. (Fig. 1). It consisted of a small irregular area (106 by 30 feet at its greatest dimensions) in a gravelly clearing among pines (*Pinus virginiana*). The degree of slope and other pertinent data for this and each of the other stands are listed in Table 1.

The second stand of this study was located at the edge of an open white oak woods near St. Paul's College, Fourth Street, NE., Washington, D.C. The woods here appears to have been artificially cleared, as there were no tall shrubs and only a few scattered forbs near the *Danthonia*, lichen, and moss vegetation which grew on a slight north-facing slope just above a three foot bank bordering the street sidewalk. A rectangular area 24 by 13 feet was chosen as representative of the Danthonia-Lichen-Moss community here.

The third and most poorly developed community considered in this study was at 3900 Harewood Road, Washington, D.C., situated on a northern slope in an open stand of oak, pine, and tulip trees. The community components occurred in irregular patches along the hillside which showed evidence of severe frost action and erosion.

A fourth stand 65 by 20 feet was studied near Sisters' College on the Catholic University campus, Washington, D.C. This community covered an open, nearly level area adjoining a pine (*Pinus virginiana*) stand and was subject to occasional mowing.

The fifth and most thriving community was located on the north side of Edgewood Road just off U.S. Highway No. 1, half a mile south of the Plant Industry Station, Beltsville, Md. The stand 60 by 12 feet was on a level area from northwest to southeast between a pine *(Pinus virginiana)* woods and an old field invaded by the bluestem broomsedge, *Andropogon virginicus*. Across the road from stand 5 north of a pine woods,

stand 6 comprised a rectangular area 75 by 12 ft.

OBSERVATIONS

The soils supporting these communities in the various areas of study ranged in texture from sandy loam to loam with a clay loam "B" layer in stands 3 and 6. They varied greatly in the percentage of gravel present with some soils showing a 40 to 60 percent gravel content, while others contained little or no gravel. Variation was also noted in color. The "A" soil layers ranged from dark gray through dark red-brown to yellowish brown. The "B" layers exhibited more uniformity, most of them being yellowish brown. A striking similarity in pH was observed among the various soil samples all of which were acid with about a pH 4.5 reaction except for one pH 5.4 reading in the top soil of stand 3.

Regardless of the differing conditions in which the community was found (difference in intensity of erosion, frost action, degree and exposure of slope, etc.), the three chief components of this community, *Danthonia*, lichens, and mosses, show a high degree of constancy (see Table 1). No single species of moss, however, is regularly associated with the *Danthonia spicata-Cladonia cristatella-Cladonia subtenuis* communities observed in this study. In stands 1 and 4 *Ceratodon purpureus* was the chief moss while *Pohlia nutans* and *Dicranella heteromalla* were most frequent in stand 2. The former moss was again frequent in stand 4 with scattered cushions of *Leucobryum albidum*. *Dicranella heteromalla* appeared infrequently again in stands 3 and 4 and frequently in stand 6. *Polytrichum commune* was found in part of stand 5. Generally where lichen cover was high, moss cover

TABLE 1.—ASSOCIATION OF DANTHONIA-LICHEN-MOSS COMMUNITIES

Analysis number	1	2	3	4	5	6	Average cover	Average frequency (percent)
Date, 1959	3–13	4–3	4–6	4–8	4–10	4–10		
Number of 2dm² samples	10	10	10	10	10	10		
Slope, degrees	NE, 5–10	N, 4	N, 20	NW, 5	NE, 0	W, 5		
Cover, percent	71.8	71.3	54.5	84.5	93.5	88.5		
Stones or bare ground	3.6	1.5	2.3	1.1	.4	.8	1.6	75
Debris	2.1	3.1	3.2	2.4	3.6	3.0	2.9	100
Total number of species	9	11	5	14	11	13		
DANTHONIA SPICATA	1.8	3.4	2.8	2.0	3.1	2.9	2.7	97
LICHENS*	4.2	1.4	3.2	3.0	3.9	2.4	3.0	97
MOSSES	.9	3.6	1.1	.9	1.8	2.8	1.9	80
Agrostis hyemalis						.2	.03	2
Andropogon virginicus				1.0	.1	.3	.2	17
Anthoxanthum odoratum		.1		.6			.1	8
Aristida dichotoma				.2	x	.2	.07	8
Digitaria sanguinalis							x	x
Juncus tenuis						x	x	2
Luzula campestris		.1					.02	2
Panicum albomarginatum	.1				.3		.07	7
Triodia flava						.2	.03	3
Antennaria plantaginifolia		.2					.03	3
Aster sp.	x						x	2
Cassia chamaechrista						.4	.07	5
Duchesnea indica				x			x	2
Liatris graminifolia						.2	.03	3
Lonicera japonica			.5				.08	8
Potentilla canadensis	x			.2	.1	.1	.07	10
Solidago nemoralis			.5	.2			.1	15
Pinus virginiana					.2	.1	.05	5
Quercus seedling						.1	.02	2

* Lichens: *Cladonia cristatella* Tuck. (common), *Cladonia subtenuis* (des Abb.) Evans (frequent), *Baeomyces roseus* Pers. (rare). Mosses: *Ceratodon purpureus* (Hedw.) Brid. (common), *Dicranella heteromalla* (Hedw.) Schimp. (frequent), *Pohlia nutans* (Hedw.) Lindb. (frequent), *Eurhynchium hians* (Hedw.) Jaeg. (infrequent), *Leucobryum albidum* (Brid.) Lindb. (infrequent), *Polytrichum commune* Hedw. (infrequent), *Dicranella heteromalla* var. *orthocarpa* (Hedw.) Par. (sparse), *Ditrichum pallidum* (Hedw.) Hampe (sparse).

FIG. 1.—Stand No. 1. A Danthonia-Lichen-Moss community in a scrub pine opening. Goldenrod is scattered. University Park, Md. April 26, 1959.

was low. In two such instances the *Danthonia* cover was also low.

In stand 5 the pink-earth lichen *Baeomyces roseus* mingled with the *Cladonia subtenuis* and rated about equal in cover. It is interesting to note that this pink-earth lichen is a soil stabilizer of wide distribution in eastern United States and is most often found on new road cuts (Hale, 1959, personal communication). The level terrain of stand 5 and the presence of this lichen along a poorly defined footpath through the center of the community may account for the high cover (93.5 percent) observed here.

The 17 percent degree of constancy noted for the broomsedge grass indicates that where it occurs adjacent to *Danthonia* communities it readily invades when a certain degree of stability is maintained by the *Danthonia*, lichens, and mosses. The other species listed in Table 1 are of such infrequent occurrence and low cover that they appear to be accidental and do not essentially belong to this community-type.

DISCUSSION AND CONCLUSIONS

It appears that disturbance such as clearing a forest, scraping off the top soil, trampling, and erosion favor the establishment of this community of *Danthonia*, lichens, and mosses. *Danthonia spicata* has a high tolerance for the infertile "raw" soil in such sites. It not only propagates by seeds in panicles, but also by large basally borne seeds called "cleistogenes" (Hitchcock, 1950). Some species of *Cladonia* and mosses are likewise hardy pioneers in these bare areas. The *Danthonia* seeds germinate in the soil, especially where some deposition is occurring in cracks of the lichen mat and in moss cushions. The mosses grow mostly during late winter and early spring and produce sporangia before the end of April if moisture is available for a sufficiently long time. Moisture and shade also apparently favor the continuance of this community, but dry weather causes cracking and breaking up of the lichen mat, thus accelerating erosion. Freezing in cold weather in a num-

ber of places causes heaving, loosening of the soil, severing the attachment of plants to the soil and increases erosion. When erosion has started, parts of the stand disintegrate rapidly, usually leaving a gravelly surface on which invasion takes place again. In some spots it appears that a cycle of invasion, growth, and degradation may be repeated several times before other species such as *Andropogon virginicus* or *Pinus virginiana* invade and cause the disappearance of most of the lichens. Similar cracking of lichen mats, especially those formed by *Diplochistes scruposus* (Schreb.) Norm., followed by erosion has been noted by the junior author in Colorado. Churchill and Hanson (1958) mention the drying and breaking of the lichen mat in the initiating of the downgrade series of cyclic changes in vegetation in the Arctic (cf. Watt, 1947).

Reduced light intensity, such as is found in openings and along edges of woods, and soil that remains wet for a considerable time after rains, is favorable for the best expression of this community. *Danthonia* does occur in open sunlight, but the lichen and moss components are poorly developed or lacking in such areas. *Danthonia* can also survive in areas where deposition is actively occurring, but mosses and lichens cannot.

As in other communities an excessive or deficient supply of plant requirements may prove limiting to the establishment and continuance of the vegetation. Too severe frost action and erosion in stand 3 may account for the poor condition of the community here. Schramm (1958) points out that soil heaving by frost action can easily occur in soil with a clay component as high as that found in this stand. The lichen mats and moss cushions are lifted by this action and offer little resistance to rain and runoff. The undermined *Danthonia* clumps soon erode away also. The most flourishing community was found in loam soil in stand 5 where the ground was level. The winds and high temperature of a Washington summer may further limit this community by causing drying of the moss and early disintegration of the lichen mats. An excessive amount of litter and debris in the form of pine needles, twigs, branches, and leaves also interferes with the growth of the plants, particularly the lichens and mosses.

The soil type in general did not seem to limit the community except where clay soils favored frost action and eliminated the pink-earth lichen, a sand-adapted species according to Nearing (1947). The *Cladonia* species and *Danthonia* appear to have a wide tolerance for different kinds of substrates. The mosses, however, seem to flourish best in the loam of the oak woods in stand 2.

From the study of these six communities it appears that the Danthonia-Lichen-Moss community is characteristic of disturbed areas in the vicinity of Washington, D.C. It occurs on a variety of soils as a pioneer in the revegetation of waste places. It is not known at present how widespread this community is. It appears important as a transitional stage in succession by stabilizing the soil and is followed by invasion and establishment of less tolerant grasses, particularly *Andropogon virginicus*, shrubs, and tree seedlings. If this invasion does not occur, the lichen mat breaks up, erosion and frost action may occur and the community is likely to deteriorate even to the bare ground stage. Thus a cyclic series of downgrade and upgrade vegetational changes may be initiated. As invasion of other species, however, does occur in time, this community performs a useful soil-stabilizing service in nature's economy in the revegetation of disturbed areas.

ACKNOWLEDGMENTS

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ACADEMY NEWS

Dr. JACOB RABINOW, president of the Rabinow Engineering Co., Inc., of Washington, D.C., has been awarded a Longstreth Medal of the Franklin Institute for his work on the magnetic fluid clutch.

Dr. WALTER RAMBERG, president of the ACADEMY in 1952 and head of the Mechanics Division at the National Bureau of Standards until this year, is now scientific attache at the American Embassy in Rome, Italy.

Dr. FRANCIS B. SILSBEE, president of the ACADEMY in 1951, retired as head of the Electricity and Electronics Division, NBS, this year.

The successful career and pleasant associations in this country of Dr. SHAN-FU SHEN of the University of Maryland were featured this summer in U. S. Information Office releases to the Far East. He was the recipient of the ACADEMY's Engineering Sciences Award at the Annual Dinner this year.

Dr. HERBERT P. BROIDA, of the Free Radicals Research Section, National Bureau of Standards, left in September to spend a year in Cambridge, England.

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